

A MONOGRAPH OF THE GENUS *AGERATUM* L. (COMPOSITAE-EUPATORIEAE)¹

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ABSTRACT

This monograph recognizes 29 species, 2 subspecies, and 14 formae in the Americas. Conventional means have been employed in determining species limits.

The genus is divided into five sections, of which two are described as new. Two species and one forma are described for the first time, and one previously described variety is accorded specific rank. Eleven taxa have been altered in rank, 17 proposed names are reduced to synonymy under other taxa of *Ageratum*, and eleven names are removed from the genus. Chromosome numbers are reported for the first time for four species, three chromosome numbers are confirmed, and corrected determinations are made for vouchers of nine previously published chromosome numbers.

Taxonomic literature, history of cultivation, economic uses, common names, geography, and generic relationships are discussed.

New keys, ecological data, and flowering and fruiting dates are included for the species and the infraspecific taxa. There are 17 distribution maps and illustrations of the new species.

The genus *Ageratum* has not been studied comprehensively since Robinson (1913b) published his revision. The lack of collections from Mexico and Central America at that time limited Robinson's work. New taxa have been described since Robinson's revision, but no key includes them. Distribution maps, ecological and chromosome data and times of flowering and fruiting for each species as well as complete descriptions were lacking in most instances. In view of the

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lack of information concerning *Ageratum* and the more abundant collections from Mexico and Central America now available, it was evident that there was need for the preparation of a new monographic treatment of the genus.

The present study of *Ageratum* covers a period of three years. I have studied several species in the field and have grown some from seed in the University of Minnesota greenhouses. However, the main descriptive portions have been drawn from approximately 2,400 specimens borrowed from 18 herbaria in the United States and Europe. I made collecting trips to Mexico in 1964, 1965, and 1966 with extensive collections resulting from the latter. Collections of type specimens have been personally studied and photographed. Chromosome numbers have been determined for several species, and the proper identification determined for numbers previously published.

This monograph treats all species of *Ageratum* over their entire ranges insofar as known, though further information is needed. Data concerning hybridization in the field, degrees of crossability, pollinators, and biological species limits are lacking. It is anticipated that these studies will be carried out later.

HISTORICAL REVIEW OF TAXONOMIC LITERATURE

One of the earliest published plant descriptions referring to an *Ageratum* is that of Hermann (1689). That this description does indeed refer to *Ageratum* is recognized from Linnaean publications (1737, 1748, 1753) in which Hermann is cited.

The name was first applied in the generic sense by Linnaeus in *Hortus Cliffortianus* (1737) and as a binomial in *Species Plantarum* (1753) in which *Ageratum* was a part of the Class *Syngenesia Polygamia Aequalis*. (According to Gray (1878), *Ageratum* is an ancient Greek or Latin name applied to some aromatic plant, probably an *Achillea*. The etymology of *Ageratum* is agreed upon by Miller (1768), Lunan (1814), Gray (1878), and L. H. Bailey (1910, 1943), all of whom derive the name from the Greek *a*, not, and *geras*, old age, referring to the long-lasting nature of the flowers. Step (1897) agrees with the etymology but wrote that the name refers to the absence of white pappus bristles so common in some members of the Compositae.)

Ageratum, in the Linnaean sense, included three species: *A. conyzoides*, *A. ciliare*, and *A. altissimum*. This alignment of species rendered the genus unnatural as *A. altissimum* is now placed with *Eupatorium urticaefolium* Reichard (Robinson, 1906a, 1906b), and *A. ciliare* was not adequately described for proper determination—its identity is uncertain. However, the plate in Plukenet (1720) which is cited by Linnaeus (1753) as *A. ciliare* shows a laterally compressed achene topped with a capillary pappus, features which exclude this species from *Ageratum*. Thus *A. conyzoides* is the only species remaining in the genus as circumscribed by Linnaeus and is designated the type.

The first major post-Linnaean study of *Ageratum* was that of Candolle (1836). He treated the genus as separate from *Coelestina* though he believed the two genera were distinguished only with difficulty. The genus was comprised of two sections in the Candollean interpretation: *Euageratum* with species having 5 distinct, acuminate, aristate pappus scales and *Pectinellum* including species

with 10 distinct, pectinate-ciliate pappus scales. In the former, Candolle placed *A. conyzoides* under which he described four varieties. All are placed in synonymy under *A. conyzoides* in the present paper except var. *mexicanum* which is placed under *A. houstonianum* Miller. Section *Pectinellum* contained *A. melissaefolium* DC., *A. matricarioides* (Spreng.) Less. and *A. domingense* Spreng. Of these, only *A. domingense* is retained in the section; *A. matricarioides* is placed in *Phania* as was done by Robinson (1913b), and *A. melissaefolium* is referred to *Trichogoniam* (Robinson, 1913b). Species originally described in *Ageratum* but possessing a coroniform pappus were transferred to *Coelestina* Cass. by Candolle.

Bentham and Hooker (1873) included a discussion of the genus and variations in the pappus. Their concept of the genus encompassed species with a cupuliform pappus but excluded *A. adscendens* Sch. Bip. and *A. glanduliferum* Sch. Bip. on the basis of their more numerous pappus scales. These species are now referred to *Oxylobus* Moc. (Robinson, 1913b).

The next treatment of the genus was that of Baker (1876). He included *Ageratum* in his tribe Ageratae which was distinguished by 5-ribbed achenes and anthers with apical appendages. The genus *Ageratum* was divided into two subgenera—*Ageratum verum* with elongate, linear, distinct pappus scales and *Coelestina* which included those species with a short, coroniform, 5-dentate pappus. Baker placed *A. conyzoides*, *A. melissaefolium*, *A. alternifolium*, *A. confertum*, *A. corymbosum*, *A. campuloclinioides*, and *A. pohlianum* in subgenus *Ageratum verum*. As interpreted today, this arrangement is an unnatural one—all species named above except *A. conyzoides* are removed from *Ageratum* because of the plumose or bristle pappus present in each (Robinson, 1913b).

Baker's subgenus *Coelestina* included *A. scorpioideum*, *A. longifolium*, *A. micropappum*, and *A. heterolepis*. Of these, *A. longifolium* and *A. heterolepis* lack a pappus and are referred to *Alomia* HBK (Robinson, 1913b).

The third major treatment was that of Hemsley (1882) based on specimens at Kew and on a large collection made by Parry and Palmer in San Luis Potosí, Mexico. Hemsley's work was meant to be, in the main, plant geography and not strictly taxonomic. Even so, the taxonomic treatment has some merit.

The genus, in the sense of Hemsley, included 24 species though he enumerated only 20 of them. *Ageratum microcephalum*, *A. salicifolium*, and *A. strictum* were described as new. He transferred *Coelestina albida*, *C. latifolia* Benth. non Cav., *C. microcarpa*, *C. paleacea*, *C. petiolatum*, *C. scabriuscula*, *C. tomentosa*, *Phania arbutifolia*, and *Isocarpha echioides* to *Ageratum*. For the most part, these species have been retained under *Ageratum*. I have reduced *A. salicifolium* to *A. corymbosum* f. *salicifolium* and placed *A. scabriuscula* in the synonymy of *A. petiolatum*. Robinson (1913b) synonymized *A. strictum* and *A. latifolium*. *Ageratum microcephalum* and *A. microcarpum* are placed in *Alomia* (Robinson, 1913b). Hemsley had included *A. adscendens*, *A. arbutifolium*, and *A. glanduliferum* which are now placed in *Oxylobus* Moc. and *A. sessilifolium* which is in *Trichocoronis* (Robinson, 1913b).

Kuntze (1891) went to the extreme in applying the principle of priority and transferred all species of *Ageratum* to *Carelia* Moehring (1736).

The most recent major contribution to the taxonomy of *Ageratum* is Robinson's (1913*b*) revision. He limited the genus to species possessing a pappus of 5 distinct scales or a cup-like crown of short, connate scales and excluded those with either a bristle pappus or that lack a pappus. The genus, as he interpreted it, contained two sections: *Euageratum* DC. with the pappus of 5 scales and *Coelestina* (Cass.) Gray with the cup-like pappus. His revision included three species new to science, seven new forms and varieties, one new name and one new combination. Synonymy, brief distribution notes, and citations of specimens were included.

I have followed Robinson's revision to a slight degree but have transferred some species from his section *Euageratum* to section *Coelestina*. I have reinstated *Ageratum domingense* in section *Pectinellum* and have placed *A. stachyofolium* in its own section. Many of Robinson's varieties have been reduced to formae especially under *A. corymbosum*. Though Robinson referred *A. echioides* to *Alomia*, I have reinstated it under *Ageratum*.

The major limitations of Robinson's revision are that it was based solely on herbarium specimens and that in some instances very few plants were available to him. This resulted in describing the same species twice, incorrect determination of individual specimens, inappropriate alliances between species, and describing forms based on corolla color.

Though Robinson (1913*b*) was the authority on *Ageratum* for more than 50 years, his revision was necessarily incomplete. There have been six species, a form, and a subspecies described since 1913 which have not been included in a previous revision of the genus.

Since 1913 the systematic literature concerning *Ageratum* has included distribution data and descriptions of new taxa. More recently, Turner and his associates and Powell and King have published chromosome numbers for several species of *Ageratum*.

HISTORY OF CULTIVATION

Ageratum conyzoides is the first species to have been cultivated in Europe. According to Schlechtendal (1857–58), it was noted by Hermann in Ghent, Belgium, prior to 1697. The earliest date of cultivation in England is 1714 where it was grown by Mary, Duchess of Beaufort, in her gardens during that year (Dandy, 1958; Miller, 1768; Schkuhr, 1808; Schlechtendal, 1857–58; Step, 1897). I believe that cultivation may have begun at least a few years prior to 1714 in England as the Duchess of Beaufort died January 7, 1714 (Dandy, 1958).

Apparently, the cultivation of *Ageratum conyzoides* had spread to Sweden by 1748 as Linnaeus considered it "tame" in his *Hortus Upsaliensis* (Linnaeus, 1748). That *A. conyzoides* was held in high regard by gardeners is apparent from Hooker's (1823) statement that it "is well deserving of a place in every stove," referring to the gardener's hothouses.

Ageratum houstonianum, first collected in 1731 in Vera Cruz, was not cultivated in Europe as an ornamental until 1822 (Step, 1897) or 1823 (Hegi, 1917), though it was known as a weed in hotbeds prior to 1768 (Miller, 1768). By 1860, it was in cultivation in Salzburg (Hegi, 1917). At present *A. houstonianum*

is the only species of the genus which is a popular garden plant. The modern horticultural varieties of *A. houstonianum* include tetraploids (personal communication, G. W. Park Seed Co.) and F_1 hybrids, which are derived by selecting progeny from crossed inbred lines of commercial *Ageratum* varieties (personal communications, American Seed Co. and Goldsmith Seeds, Inc.).

MEDICINAL AND ECONOMIC USES

Ageratum conyzoides plays a role in folk medicine over much of its range. Holland (1922) reports *A. conyzoides* as useful externally for treatment of Craw-craw, a contagious, parasitic, pustular skin disease common among Negroes of West Africa, and internally for treatment of fever in Yoruba-land. The same cures are reported by Dalziel (1937) in Nigeria. The plant is also used externally as treatment of Craw-craw and chronic ulcer, and internally as an emetic and for intra-uterine problems, in Sierra Leone (Dalziel, 1937). The juice is an eye medicine in the Gold Coast, an external remedy for pneumonia in children in Liberia, a purgative enema in the Cameroons, and a treatment for sleeping sickness in Portuguese Congo (Dalziel, 1937).

Ageratum conyzoides is highly prized as a remedy for non-menstrual vaginal hemorrhage in South America and as a remedy for prolapsus ani in India (F. M. Bailey, 1906). Leaves scorched over a fire are placed on fresh wounds in Malayasia (Steenis, 1947-48). Natives of Borneo have used leaves on skin boils and wounds due to dog or crocodile bites and as a remedy for stomach ache (Koster, 1935).

Additional medical uses have been culled from herbarium labels. *Ageratum conyzoides* functions as a remedy for stomach ache in Colombia and Venezuela (Fosberg 19250, US). The leaves are used medicinally for cuts in the Caroline Islands (Fosberg 32054, NY), and an unspecified part of the plant is used as remedy for gonorrhea in El Salvador (Standley 19220, US), in an infusion as a syrup for sore throat in Chiapas (Matuda 16841, F, NY) and as an anticatarrhal in Colombia (Perez-Arbelaes, 1956). In Canton, China, the whole plant is placed in water, allowed to decay and then fed to small fish which are raised as food (Hu, 1956).

An infusion prepared by boiling *Ageratum echinoides* is drunk for malarial treatment in Guatemala (Steyermark 51500, NY).

The leaves of *Ageratum gaumeri* are used to check nosebleed in Yucatan (Millspaugh, 1903), and *A. houstonianum* is a remedy for sore throat in Guatemala (Goll 238, NY, US).

The value of *Ageratum conyzoides* as a medicinal plant is seemingly due to alkaloids which have a vaso-constrictor action similar to that of ergot (Chevalier, 1910). The medicinal value of *A. echinoides*, *A. gaumeri*, and *A. houstonianum* may be alkaloidal in nature, too, though I am not aware of any studies indicating this.

Ageratum littorale is reported to be used as treatment for unspecified illnesses in Mexico (Martinez, 1933), but Martinez must be referring to some other plant—*A. littorale* does not occur in Mexico.

COMMON NAMES

The genus is known as *agerate* in French, *Leberbalsam* in German and by its Latin name among horticulturists and gardeners, though seed packets of *Ageratum houstonianum* are sometimes sold under the name "Floss Flower," the same name applied to *A. conyzoides* in India (Fyson, 1932). There have been numerous names applied to horticultural varieties of *A. houstonianum*, the only species cultivated to any extent in the United States. These names, which are very descriptive, include "Summer Skies," "Blue Blazer," "Blue Mink," "Blue Fox," and "Pure White." Plants sold under the name "Hardy Ageratum," *Ageratum lasseauxii*, and Perennial Ageratum are in the genus *Eupatorium*; those sold as "Golden Ageratum" are *Lonas annua* Vines & Druse (Sims, 1822, and personal communication from F. A. Swink, The Morton Arboretum).

Wild *Ageratum houstonianum* is referred to as "Yerba de Zopilote" (Kerber 302, BM, US) and "Flor de Garrapata" (Kelly 908, US) in Vera Cruz, its native habitat.

Ageratum corymbosum sens. lat. is known as "Flat-top Ageratum" in Texas (Gould, 1962) and in Spanish as "Cielitos" (Robinson, 1913b). Reiche (1926) gives "Mota morada" as a common name in Mexico, a name applied to *A. gaumeri* also.

"Frijolito" is the name applied to *A. echinoides* (Steiermark 51500, NY), "Mota" is used to refer to *A. rugosum* (Standley 58050, NY) and "Mejorano" for *A. houstonianum* (Goll 238, NY, US) in Guatemala.

Ageratum gaumeri is known as "Tucan" (Steere 1009, GH, MICH, US), "bakelus," "Mota," "Mota morada," "Serenó," and "Flor de San Juan" (Millspaugh, 1903) in the Yucatan Peninsula. "Serenó" also refers to *A. houstonianum* in Mexico (Rovirock 693, NY).

"Santa Lucia" is the name given to the genus as a whole in Costa Rica (Standley, 1938) and more specifically to *A. oerstedii* (Holway s.n., MIN), *A. conyzoides* (Standley, 1938), and to *A. standleyi* in Honduras (Molina 14686, F). This name also refers to species of *Alomia*.

Ageratum standleyi is also known as "Azullilo" in Honduras (Standley 1498, F). *Ageratum petiolatum* is referred to as "Conejito" in Nicaragua (Maxon 7661, US).

Ageratum conyzoides, a widespread tropical weed, has received names too numerous to list completely. However, I have selected some of the names as examples. "Mejorana" is the name used in El Salvador (Standley, 1928; Calderon 155, MO, US; Standley 19220, US) and Guatemala (Cook & Griggs 560, US), while *A. conyzoides* is known as "Mentrasto" in Brazil (Macedo 173, MO; Blanchet 875, NY) and Puerto Rico (Cook & Collins, 1903; Stahl, 1937). "Manrubio" is the common name in Colombia (Daniel 526, US). Examples of descriptive names include "Hierba del perro" or herb of the dog in El Salvador (Padilla 249, US), "Hierba del Zorro" or herb of the fox or cunning fellow in Argentina (Montes 1797, US), and "catinga de bode" which is translated as "bad smell of he-goat" in Brazil (Perez-Arbelaez, 1956). The malodorous nature is also the basis for the names "Billy Goat Weed" (Dalziel, 1937; Russell s.n., UC) and "Billygoat Plant" (F. M. Bailey, 1906) in Australia and "Goat Weed" in Ceylon (Cooke,

1908; Trimen, 1895). The Chinese characters for *A. conyzoides*, when translated, read "flower with odor of salty shrimp" (*To, et al.* 97L, UC), again alluding to the disagreeable odor.

GEOGRAPHIC DISTRIBUTION

Ageratum is restricted to the Americas and adjacent West Indies except for *A. conyzoides* subsp. *conyzoides*, a weed introduced pantropically. Of the 39 taxa recognized in the present paper, the vast majority are in Mexico, Central America, the West Indies, and south Florida. Only four taxa occur in South America, one of these being *A. conyzoides* subsp. *conyzoides*. The genus is widely distributed in Mexico especially in the Temperate Pine-Oak Forest Zone of Leopold (1950). However, the distribution of individual taxa is often localized in a relatively small area. For example, five taxa are localized in Yucatan; *A. oerstedii* is endemic to Costa Rica. Except for *A. conyzoides* subsp. *conyzoides*, ranges of the South American taxa are restricted as well.

Wind is quite probably an important means of dispersal for all species. The fruits are light and easily blown even by gentle air currents from an office fan. Those fruits with a pappus of spreading scales presumably have additional air buoyancy.

Man has played a role in dispersal and introduction of *A. conyzoides* subsp. *conyzoides* at least in the Philippine Islands. Galleons leaving Acapulco and Navidad, Mexico, bound for Manila carried seeds that formed the basis for the plants which are very abundant in the Philippines today (Merrill, 1912). The form of the fruits also aids in their passive dispersal by man, as the fruits are not only small but prismatic. I have often found fruits embedded among the fibers of clothing after a day of studying *Ageratum*. Some are equipped with stiff hairs along the angles which aid in attaching them to clothing. Man's cultivation of crops in the tropics has aided in the spread of this weed as it readily establishes itself in open, worked soil.

GENERIC-INTERGENERIC RELATIONSHIPS

Ageratum is placed in the tribe Eupatorieae, characterized by its tubular flowers which are all alike and are never yellow, anthers basally blunt, and style branches terete, clavate, papillate and stigmatic near the base.

Ageratum is apparently closely related to *Alomia* which it closely resembles in habit, habitat, and to a degree in distribution. These genera are distinguished by the lack of a pappus in *Alomia*. Heretofore, *Ageratum* was considered to be closely related to *Oxylobus*, but study of data gathered from chromosome numbers, morphology, and ecology suggests a more distant relationship.

SPECIES CONCEPT

Species and lower taxa are delimited primarily on morphological bases. Geographical distribution and chromosome numbers have been employed to supplement morphology when appropriate.

For the most part, the species are very distinct morphologically. Introgression and consequent blurring of species limits, if it is occurring, is not evident in this

genus. Though cytodemes of tetraploid plants do occur, these have not been recognized nomenclaturally unless morphological differentiation accompanies the polyploidy.

The major morphological subunits of the species which have a distinct geographic area and between which there is little or no chance of transfer of germ plasm are referred to here as subspecies. Only two subspecies, between which the barrier to transfer of germ plasm is genetic, are recognized in this paper—*A. conyzoides* subsp. *conyzoides* and *A. conyzoides* subsp. *latifolium*. The first is a tetraploid, while the latter is a diploid.

Formae are recognized when consistent, minor, vegetative variations which do not have a distinct geographic area occur. Formae based on corolla color have not been maintained. This character is extremely variable, and it becomes exceedingly arbitrary and subjective if the varying shades are given names. No deterrent to gene exchange between formae of a single species is implied by a form name.

CHROMOSOME NUMBERS

The basic chromosome number for the genus is $x = 10$. Natural tetraploids, $n = 20$, are reported for nine taxa. A triploid, $3n = 30$, is reported for the first time for the genus.

It is common to find polyploid chromosome races within a normally diploid species of *Ageratum*. Usually, in *Ageratum*, the diploids and polyploids are so similar that they are indistinguishable by means other than actually counting chromosomes. I have measured pollen grains, stomatal guard cells, and other morphological characters on specimens for which the ploidy level is known. For the most part, there is no difference between features from $2n$ and $4n$ plants, and thus the polyploids can be termed "semi-cryptic" (Davis & Heywood, 1963). Due to the similarities between polyploids and diploids, no attempt is made to set apart chromosome races within a taxon except in *A. conyzoides sens. lat.*

Ageratum conyzoides subsp. *conyzoides*, a tropical, tetraploid weed, is very similar to *A. conyzoides* subsp. *latifolium* which is diploid. The main gross morphological character that distinguishes these taxa is the setiferous pappus scales of *A. conyzoides* versus truncated scales in subsp. *latifolium*. Though not always consistent, known references to chromosome numbers indicate that the tetraploid plants produce a setiferous pappus and that the $2n$ plants have a truncated one.

SYSTEMATIC TREATMENT

***Ageratum* L., Sp. Pl. 2: 839. 1753.**

Carelia Adans., Fam. Pl. 2: 123. 1763.

Annual *herbs* and perennial *shrubs* 0.45–24 dm tall; *roots* fibrous or a tap-root, at times adventitious; *stems* woody or herbaceous, rarely succulent, erect, repent, decumbent, simple or branched, puberulous, pilose, scabrous, glandular-villous or glabrous, glandular-atomiferous to eglandular, sap watery; *leaves* opposite or alternate, petioled or sessile, firm or more or less membranaceous, ovate, elliptic, lanceolate, linear, deltoid, orbicular or cordate, 0.5–10(–13) cm

TABLE 1. Haploid chromosome numbers reported for the genus *Ageratum*.

Taxon	Haploid number	Locality and voucher	Source
<i>A. albidum</i>	$n = 20$	MEXICO. OAXACA: Monte Alban, <i>King</i> 3490 (DS, MICH, NY, TEX, UC, US).	Turner, Ellison & King, 1961.
<i>A. conyzoides</i> subsp. <i>conyzoides</i>	$n = 10$	None given.	Ishikawa, 1911, 1916.
	$n = 10$	None given.	Mehra <i>et al.</i> , 1966.
	$n = 20$	PANAMA. Concepción, <i>King</i> 5286 (TEX, UC, US).	Turner & King, 1964.
	$n = 20$	PANAMA. COCLE: El Valle, <i>King</i> 5327 (TEX, UC, US).	Turner & King, 1964.
	$n = ca. 20$	PANAMA. Cerro Azul, <i>King</i> 5248 (TEX, US).	Turner & King, 1964.
	$n = 20$	UGANDA. <i>Lewis</i> 6028 (TEX).	Turner & Lewis, 1965.
	$n = 20$	TANGANYIKA. <i>Lewis</i> 6060 (MO, TEX).	Turner & Lewis, 1965.
	$n = 20$	KENYA. <i>Lewis</i> 5912 (MO, TEX).	Turner & Lewis, 1965.
	$n = 20$	SIERRA LEONE. <i>Harvey</i> 104 (K).	Löve, 1966.
	$n = 20$	DOMINICA.	Powell & King, 1969.
<i>A. corymbosum</i> f. <i>corymbosum</i>	$n = 20$	MEXICO. MICHOACAN: <i>King</i> 3644 (DS, MICH, NY, TEX, UC, US).	Turner, Ellison & King, 1961. ^c
	$n = 11$	MEXICO. MICHOACAN: E of Jiquilpan, <i>King & Soderstrom</i> 4901 (MICH, TEX, UC, US).	Unpublished, data from herbarium labels.
	$n = 10$	MEXICO. OAXACA: NE of Huajuapán, <i>King</i> 3544 (MICH, TEX).	Turner, Powell & King, 1962. ^d
	$n = 10$	MEXICO. PUEBLA: W of Izucar de Matamoros, <i>King</i> 2933 (MICH, TEX).	Turner, Powell & King, 1962.
	$n = 10$	GUATEMALA. E of Chiantla, <i>Owney & Muggli</i> 3971 (MIN).	Author.
	$n = 15$	MEXICO. MICHOACAN: E of Morelia, <i>Owney & Muggli</i> 3948 (MIN).	Author.
<i>A. corymbosum</i> f. <i>albiflorum</i>	$n = 10$	MEXICO. CHIAPAS: SE of Comitán, <i>King</i> 3045 (TEX).	Turner, Powell & King, 1962. ^e
	$n = 20$	PERU. <i>Wurdack</i> 443 (NY, TEX, US).	Unpublished, data from herbarium labels.
	$n = ca. 17$	GUATEMALA. <i>King</i> 3153 (TEX).	Unpublished, data from herbarium labels.
	$n = 20$	THAILAND. <i>King</i> 5528 (TEX), 5537 (TEX, UC), 5574 (TEX), 5577 (TEX, UC), 5584 (TEX).	Unpublished, data from herbarium labels.

TABLE 1. Haploid chromosome numbers reported for the genus *Ageratum*.
(Continued from page 14)

Taxon	Haploid number	Locality and voucher	Source
<i>A. conyzoides</i> subsp. <i>latifolium</i>	$n = 10$	MEXICO. HIDALGO: King 4226 (F, MICH, NY, TEX, UC).	Turner, Powell & King, 1962. ^a
	$n = 10$	MEXICO. PUEBLA: King 4140 (MICH, NY, TEX, UC).	Turner, Powell & King, 1962.
<i>A. corymbosum</i> f. <i>euryphyllum</i>	$n = 20$	MEXICO. SAN LUIS POTOSI: La Capilla, Rock 456 (TEX).	Turner, Beaman & Rock, 1961. ^b
	$n = 10$	MEXICO. OAXACA: S of Tehuacan, Powell & Edmondson 666 (F, MICH, TEX).	Powell & Turner, 1963. ^f
	$n = 10$	MEXICO. JALISCO: W of Sahuayo, Powell & Edmondson 841 (TEX).	Powell & Turner, 1963. ^g
	$n = 10$	MEXICO. DURANGO: W of Revolcaderos, Ownbey & Muggli 3927 (MIN).	Author.
<i>A. corymbosum</i> f. <i>salicifolium</i>	$n = 10$	MEXICO. JALISCO: W of Guadalajara, Powell & Edmondson 866 (F, MICH, TEX).	Powell & Turner, 1963. ^h
	$n = 20$	MEXICO. DURANGO: N of Durango, King 3750 (DS, MICH, NY, TEX, UC, US).	Unpublished, data from herbarium labels.
<i>A. echioides</i>	$n = 20$	MEXICO. CHIAPAS: SE of San Cristobal de las Casas, Ownbey & Muggli 3986 (MIN).	Author.
<i>A. elassocarpum</i>	$n = 11 \pm 1$	MEXICO. CHIAPAS: SE of Las Cruces, King 3112 (DS, MICH, NY, TEX, UC, US).	Turner, Powell & King, 1962. ⁱ
<i>A. guatemalense</i>	$n = 10$	GUATEMALA: S of Huehuetenango, Ownbey & Muggli 3972 (MIN).	Author.
<i>A. houstonianum</i>	$n = 10$	None given.	Cooper & Mahoney, 1935.
	$n = 20$	None given.	Morrison & Rajhathy, 1960.
	$n = 10$	MEXICO. VERA CRUZ: W of Cordoba, King 2360 (MICH, TEX).	Turner, Ellison & King, 1961.
	$n = 10$	MEXICO. MORELOS: S of Cuernavaca, King 4160 (MICH, TEX, UC).	Turner, Powell & King, 1962.
	$n = 10$	GUATEMALA. S of Goban, King 3311 (DS, MICH, TEX, UC).	Turner, Powell & King, 1962.
<i>A. houstonianum</i> f. <i>isochroum</i>	$n = 10$	MEXICO. CHIAPAS: San Quintin, Breedlove 9135 (MICH).	Unpublished, data from herbarium labels.

TABLE 1. Haploid chromosome numbers reported for the genus *Ageratum*.
(Continued from page 15)

Taxon	Haploid number	Locality and voucher	Source
<i>A. nelsonii</i>	$n = 10$	MEXICO. CHIAPAS: E of Oaxaca-Chiapas border along Rte. 190, King 2981 (MICH, TEX).	Turner, Powell & King, 1962. ¹
	$n = 10$	MEXICO. CHIAPAS: E of Oaxaca-Chiapas border along Rte. 190, King 2751 (MICH, TEX).	Turner, Powell & King, 1962. ^k
<i>A. petiolatum</i>	$n = 10$	PANAMA. N of Concepción, King 5289 (TEX, UC).	Turner & King, 1964. ¹
<i>A. platypodum</i>	$n = 20$	MEXICO. JALISCO: E of Tapalpa, Ownbey & Muggli 3941 (MIN).	Author.
<i>A. rugosum</i>	$n = 20$	GUATEMALA. N of Salama, King 3291 (TEX.)	Turner, Ellison & King, 1961. ^m
	$n = 20$	GUATEMALA. N of Palen, Ownbey & Muggli 3976 (MIN).	Author.
<i>A. tomentosum</i>	$n = 10$	MEXICO. PUEBLA: N of Puebla-Oaxaca border, King 3548 (NY, TEX, UC, US).	Turner, Ellison & King, 1961.

^a Published as *A. latifolium* Cav.^b Published as *A. corymbosum* Zuccag.^c Published as *A. cf. lucidum* Robins.^d Plus fragments.^e Published as *A. corymbosum* Zuccag.^f Published as *A. albidum* (DC.) Hemsl.^g Published as *A. cf. corymbosum* Zuccag.^h Published as *A. salicifolium* Hemsl.ⁱ Published as *A. cf. paleaceum* (Gay) Hemsl. var. *paleaceum*.^j Published as *A. cf. tomentosum*.^k With fragments, published as *A. paleaceum* (Gay) Hemsl. var. *nelsonii* Rob.^l Published as *A. corymbosum* Zuccag.^m Published as *A. corymbosum* Zuccag.

long, 0.25–9 cm wide, base obtuse, cordate, truncate, apex acute to acuminate, margin revolute or plane, crenate, dentate or shallowly lobed to entire, ciliate, scabrous or glabrous, upper surface usually green to dark green or brown, pilose, scabrous, glandular-punctate and/or atomiferous or eglandular to glabrous, at times rugulose, lower surface pale green to gray, densely to sparingly pilose, glandular punctate and/or atomiferous to eglandular, 3-veined or the venation reticulate, rarely palmate; stomatal apparatus on the lower leaf surface of the paracytic type (Essau, 1960); *petioles* 0.2–3(–6) cm long, pilose, glandular-atomiferous to glabrous, at times narrowly winged distally; *inflorescences* in compact to open corymbiform clusters, in heads borne singly or in an irregular panicle, the 3–10(–30 or more) heads borne on pilose, glandular or eglandular, bracteate peduncles 0.3–8.5(–15) cm long; *involucres* campanulate, hemispherical or turbinate, bracts bi- or less commonly triseriate, firm or membranaceous, 2- or 4-ribbed or smooth and merely nerved, lanceolate, lanceolate-oblong, ovate or spatulate, 2–6.85 mm long, outer bracts 0.5–1.55 (0.4–1.35) mm wide, green to variously tinged with red or purple, pilose and glandular-atomiferous to glabrous, margin green to scarious, entire to variously erose apically, ciliate, scabrous or glabrous, apex acuminate, acute or rounded, ciliate or glabrous; *receptacle* conical, naked or less commonly paleaceous, paleae resembling involucre bracts; *corollas* funnelform or tubular, 1.1–3.75 mm long, pilose, pu-

berulent, scabrous, glandular-atomiferous or glabrous, tube and narrow throat pale green or white, the 5 erect or spreading deltoid lobes lavender, lilac, mauve, violet, blue, gray or white; *style* branches bifurcate, terete, clavate, papillate, stigmatic area near base, same color as corolla lobes; *anthers* apically appendaged; *pollen* spheroidal, echinate, tectate, tricolporate or rarely tetracolporate; *achenes* 5-angled, prismatic, dark brown to black, 1–2.75 mm long, glabrous or scabrous on angles or throughout, with whitish carpodium at base or carpodium lacking; *pappus* of 5–6 free, membranous, flattened, elongate, oblong scales 0.23–3.5 mm long, with or without setae, or pappus coroniform or cup-shaped and 0.1–0.55 mm long, margin entire, undulate or setiferous; recorded chromosome numbers $n = 10$, $n = 20$, $3n = 30$.

Type species: *Ageratum conyzoides* L.

KEY TO SECTIONS OF *AGERATUM*

1. Stems erect or decumbent; leaves opposite or alternate, variously shaped but not orbiculate-cordate; involucre bracts 2- or 4-ribbed or 5-nerved; corolla tube very gradually expanded toward the throat; achenes with whitish carpodium or the carpodium lacking; pollen grain wall thin, ca. 2–3 μ thick 2
2. Leaves alternate, short petiolate; involucre bracts 4-ribbed; achenes glabrous, basally sharp-pointed, carpodium lacking; pappus coroniform — Section IV. *Stachyofolium*
2. Leaves opposite, short or long petiolate; involucre bracts 2-ribbed or 5-nerved; achenes glabrous or scabrous throughout or at least on the angles, carpodium conspicuous or inconspicuous; pappus of 5 or rarely 6 basally free, usually setiferous scales or the pappus coroniform 3
3. Annual or perennial herbs; pappus of 5 to 6 basally free, usually apically setiferous scales; achenes scabrous at least on the angles or throughout; carpodium conspicuous or inconspicuous; receptacle naked or paleaceous 4
4. Achenes scabrous only along the angles, or if on the sides, the hairs not yellow; carpodium conspicuous; involucre bracts firm, 2-ribbed, narrowly lanceolate, lanceolate or oblong, the apex acute; receptacle naked Section I. *Ageratum*
4. Achenes scabrous throughout, the hairs conspicuously yellow and pointed upward; carpodium inconspicuous, involucre bracts membranaceous, 5-nerved, widely ovate, the apex broadly rounded; receptacle paleaceous Section V. *Perplexans*
3. Woody or herbaceous perennials; pappus coroniform, cup-like or if the margin setiferous, the setae basally connate; achenes glabrous, carpodium conspicuous; receptacle paleaceous or naked Section II. *Coelestina*
1. Stems repent; leaves opposite, orbiculate-cordate on vertically elongate petioles; involucre bracts unribbed; corolla tube abruptly expanded toward the throat; achenes lacking a carpodium; pollen grain wall ca. 5 μ thick Section III. *Pectinellum*

Section 1. *Ageratum*

Euageratum DC., Prod. 5: 108. 1836.

Ageratum verum Baker in Martius, Fl. Bras. 6 (2): 194. 1876.

Annual or perennial *herbs*; *roots* fibrous, at times adventitious; *leaves* opposite, ovate, elliptic, linear, lanceolate, oblong or deltoid, variously pubescent to glabrous; *inflorescences* grouped in corymbiform clusters or borne singly; *involucre* bracts 2- or 3-seriate, narrowly lanceolate, lanceolate or oblong, apex gradually or abruptly contracted, margin entire or apically erose or fimbriate, stipitate-glandular to glabrous; *receptacles* naked; *corollas* tubular, varying shades of blue and lavender or white; *achenes* scabrous on angles; *carpodium* conspicuous; *pappus* of 5, rarely 6, scales basally free and usually setiferous.

Type species: *Ageratum conyzoides* L.

Species in this section occur in British Honduras, the Yucatan Peninsula, northern South America, southern Mexico, Central America, and the West Indies. One species is a pan-tropic weed. Flowering and fruiting occur year around as local conditions permit.

KEY TO SPECIES IN SECTION *AGERATUM*

1. Heads 3–18, grouped in a terminal corymbiform cluster; peduncles less than 4 cm long; leaves firm, at least not membranous, ovate, elliptic, linear, lanceolate, oblong or deltoid; pappus scales abruptly contracted apically to a scabrous or pectinate, coarse seta or the pappus scales truncated and variously pectinate to entire 2
2. Plants erect; leaves elliptic or linear 3
 3. Leaves elliptic, 3–6 cm long, 0.8–2 cm wide; plants 3–5 dm tall; generally pubescent throughout; coastal regions, British Honduras 1. *Ageratum ellipticum*
 3. Leaves linear, 2.3–5 cm long, 0.25–0.5 cm wide; plants 2–5 dm tall, generally glabrous throughout; tropical pinelands, British Honduras 3. *Ageratum peckii*
2. Plants erect or decumbent-repent; leaves ovate, lanceolate, oblong or deltoid 4
 4. Plants decumbent-repent, less commonly erect; leaves lanceolate to oblong, 4.5–6.7 cm long, 0.5–1.4 cm wide, glabrous; involucre bracts 3-seriate, firm, glabrous; stem glabrous or sparingly pilose-puberulent at nodes; wet areas and fresh water ponds, British Honduras 2. *Ageratum radicans*
 4. Plants erect, less commonly decumbent; leaves ovate to deltoid, pilose and glandular; involucre bracts biseriate, less firm, pilose or sparingly so to stipitate-glandular; stems decidedly puberulous-pilose to lanate-woolly especially above; Mexico, Central America, northern South America or a pan-tropic weed 5
 5. Leaves ovate to deltoid, the base cordate to truncate; involucre bracts narrowly lanceolate, the apex long-acuminate, entire, conspicuously pilose, and stipitate-glandular; southern Mexico, British Honduras, Guatemala, West Indies 4. *Ageratum houstonianum*
 5. Leaves ovate, the base obtuse, never cordate or truncate; involucre bracts wide, oblong, sparingly pilose to glabrous, eglandular, the apex abruptly contracted to less commonly gradually acuminate, the margin erose to variously fimbriate, rarely entire 5. *Ageratum conyzoides*
1. Head single, terminal; peduncles 4.5–15 cm long; leaves thin, ovate; pappus scales blunt, variously fimbriolate apically, rarely with a fine apical seta or pappus minute and appearing coroniform 6. *Ageratum gaumeri*

1. *Ageratum ellipticum* Robins., Contr. Gray Herb. 90: 5. 1930.

Holotype: BRITISH HONDURAS: Honey Camp, Lundell 512 (GH); isotypes, DS, F, K, MO, NY.

Annual, 3–5 dm tall; roots fibrous; *stems* erect, branched, short pilose, at least at nodes, to nearly glabrous; *leaves* elliptic, becoming lanceolate near inflorescences, (3.1–)3.5–4.5(–6) cm long, (0.8–)1.1–1.8(–2) cm wide, apex acute, base more or less gradually attenuate to the petiole, margin revolute, entire to remotely crenate, ciliate to rarely glabrous, both surfaces pilose to nearly glabrous, the 3 longitudinal veins prominent; *petioles* 0.5–2 cm long, marginally pilose; *inflorescences* of 3–5(–6) heads borne on bracteolate, short puberulent-pilose peduncles ca. 1 cm long; *involucre* campanulate, bracts triseriate, lanceolate, 3–3.5(–4) mm high, 0.5–0.75 mm wide, green, glabrous, prominently 2-ribbed, margin entire, at times minutely ciliate; *corollas* tubular, 1.65–2 mm long, glabrous to minutely scabrous, tube and narrow throat pale green to white, 5 lobes acute, erect, blue to lilac; *achenes* dark brown to black, 1–1.15(–1.25) mm

long, white puberulent-scabrous on angles and sides; *pappus* of 5, rarely 6, lanceolate, pale tan scales, apex tapering to a scabrous elongate seta, margin entire to variously fimbriate, entire scale 1.4–1.9 mm long.

Ageratum ellipticum is a distinct, apparently rare, endemic species in British Honduras. Robinson (1930), in describing the species, called attention to its similarities to *A. radicans*. Though indeed similar and seemingly closely related, these taxa are readily distinguishable. The widely elliptic, pilose leaves, pilose stems and shorter achenes are constant features of *A. ellipticum* that set it apart from *A. radicans*. *Ageratum ellipticum* is similar to *A. peckii* in the achenes, pappus and corollas but is distinguishable by the general pubescence, the larger elliptic leaves and larger size of the former.

This species is endemic to the coastal area of British Honduras. Specimens studied were collected in August and September; buds, flowers, and fruits were present.

BRITISH HONDURAS. Monkey River, near Jenkins Creek, *Gentle* 4135 (F, GH, MICH, MO, NY); vicinity of Tower Hill, *Karling* 31 (F, GH, US); Honey Camp, *Lundell* 512 (DS, F, GH, K, MO, NY); Pine Ridge, near Honey Camp, *Meyer* 127 (F, K).

2. *Ageratum radicans* Robins., Proc. Amer. Acad. Arts 47: 192. 1911.

Holotype: BRITISH HONDURAS: Pond near Manatee Lagoon, *Peck* 99 (GH); isotype, K; photograph, MIN.

Annual, 2.7–7 dm tall; *roots* fibrous, adventitious at lower nodes if stem repent; *stem* branched, erect or procumbent to repent, glabrous to sparingly pilose-puberulent at nodes and near inflorescences; *leaves* glabrous to sparingly pilose at least on veins, lanceolate to oblong, 3.4–6.2(–8) cm long, (0.4–)0.61–1.7(–1.9) cm wide, tip acute, base gradually attenuate to a narrowly winged petiole, margin revolute, entire to remotely crenate on distal two-thirds, veins longitudinal, mid-vein conspicuous as seen from beneath; *petioles* ca. 1.3 mm long, glabrous to pilose; *inflorescences* of 3–5 heads borne on puberulent bracteolate peduncles 0.5–1 cm long; *bracteoles* alternate, subulate, glabrous to ciliate along margin; *involucres* campanulate, bracts firm, triseriate, prominently 2-ribbed, lanceolate (2.5–)3–4(–4.5) mm high, (0.4–)0.5–0.85 mm wide, green, glabrous, margin herbaceous to scarious, entire, glabrous to minutely ciliate, apex acute; *corollas* tubular to narrowly funnelform, 1.8–2.25(–2.45) mm long, glabrous throughout, the 5 obtuse lobes purplish-lavender to bright blue; *achenes* dark brown to black, (1.0–)1.15–1.35(–1.5) mm long, puberulent on angles, carpopodium white; *pappus* of 5 (rarely 6) whitish, lanceolate scales, (1.45–)1.75–2.05(–2.35) mm long, margin of scales fimbriate, apex gradually attenuate to an elongate scabrous seta.

Robinson (1911) described this species as “*prostratum reptans*” from seeing only one specimen. After having seen a number of collections, it is evident that Robinson drew attention to an uncommon growth habit; the usual form is a conspicuously upright stem. Some plants, however, may become prostrate and form roots at the lower nodes.

Ageratum radicans is undoubtedly closely related to *A. ellipticum* as both species are very similar in gross morphology, distribution, and ecology. These

species are commonly confused by collectors and herbarium curators as is evident from the number of misapplied names on herbarium labels. However, *A. radicans* is distinguished from *A. ellipticum* by the overall glabrous condition and the lanceolate to oblong leaves of the former. The lanceolate leaves are also the best means to distinguish *A. radicans* from *A. peckii*, in which the leaves are linear.

Ageratum radicans is endemic to British Honduras in wet areas and fresh water ponds. Flowers and fruits are present in December, January, and February; and again in July and August.

BRITISH HONDURAS. Butcher Burn, Sibun River, *Bartlett* 11389 (GH, K, MICH, US); Mondes, *Campbell* 58 (K); Bakers, near Belize River, 18 miles from Belize, *Espat* 46 (F); Maskall Pine Ridge, *Gentle* 1355 (K, MICH, MO, NY, TEX, US); Gracie Rock, Sibun River, *Gentle* 1757 (K, MICH, MO, NY, US); Augustine, *Hunt* 43 (BM, US); Mountain Pine Ridge, *Lamb* 132 (K); Orange Walk, *Lundell* 70 (F); Baker's Pine Ridge, *Lundell* 3821 (MICH, US), 4705 (NY, UC, US); pond near Manatee Lagoon, *Peck* 99 (GH, K); All Pines, *Schipp* 611 (BM, F, GH, K, MICH, MO, UC).

3. *Ageratum peckii* Robins., Proc. Amer. Acad. Arts 47: 192. 1911.

Holotype: BRITISH HONDURAS: Pine Ridge near Manatee Lagoon, *Peck* 80 (GH); isotype, K.

Annual or *perennial*, ca. 2–5 dm tall; *roots* fibrous; *stems* erect, branching, glabrous, woody at base, bark dark red; *leaves* numerous, glabrous, linear-oblong, (2.3–)3–5 cm long, (0.25–)0.3–0.5 cm wide, tip rounded to acute, base long attenuate to the slightly winged petiole, margin entire to remotely crenate (under 15× magnification), lower surface with (1–)3–5 longitudinal veins, mid-vein more or less conspicuous; *inflorescences* corymbiform, the 3–5 heads borne on glabrous to sparingly puberulent bracteolate pedicels 0.3–2 cm long; *bracteoles* alternate, subulate, 1.5–3 mm long, merging with involucre bracts; *involucre* campanulate, biseriate, bracts prominently 2-ribbed, green to brown, glabrous, lanceolate to linear, (3.1–)3.6–3.8 mm high, (0.45–)0.55–0.65 mm wide, tip gradually acuminate, margins entire; *corollas* tubular or gradually expanded upward, (1.7–)2.2–2.3 mm long, glabrous, the obtuse lobes purple to blue; *achenes* dark brown to black, 1–1.25(–1.45) mm long, glabrous to sparingly puberulent; *pappus* of 5 upright, lanceolate, tawny scales, 1.5–2.2 mm long, margin variously fimbriolate, apex abruptly tapered to an elongate scabrous seta.

Ageratum peckii is one of the lesser known species in the genus. I have seen only three collections during the course of this study. However, even with few data upon which to base a decision, the plants designated *Ageratum peckii* comprise a good species. The glabrous, elongate, nearly entire leaves and the erect habit serve to distinguish this species from all other taxa. See also the discussion under *A. ellipticum* and *A. radicans*.

This species is endemic to British Honduras in tropical pine lands. Flowers and fruits are present in February, July, and August.

BRITISH HONDURAS. El Cayo District, Mountain Pine Ridge, *Bartlett* 11696 (GH, K, MICH, US); 12 miles N of Belize, Pine Ridge, *O'Neill* 8383 (F, GH, NY, UC); Pine Ridge near Manatee Lagoon, *Peck* 80 (GH, K).

4. *Ageratum houstonianum* Miller, Gard. Dict. Ed. 8. 1768.

Holotype: MEXICO: Vera Cruz, *William Houston s.n.* (BM, not seen); photographs, MIN, NY, UC.

Annual, (2.5–)3–7(–9) dm tall; *roots* fibrous, adventitious at lower nodes if stem decumbent; *stems* simple or branched, especially above, erect or decumbent, reddish to green, glandular-villous to lanate above, hairs white to yellowish; *leaves* opposite, at times alternate above, ovate to deltoid, 2.4–8.6(–9.5) cm long, (1.7–)2.9–6.5(–8) cm wide, apex rounded or acute, base cordate to truncate, margin crenate or rarely dentate, more or less ciliate, upper surface dark green, pilose, hairs scattered or dense, especially over the veins, lower surface pale green, penninerved, densely pilose, especially over veins, to nearly glabrous; *petioles* 0.6–3.5 mm long, densely white pilose, especially on upper ones; *inflorescences* terminal, the 5–15 heads borne in tight or open cymose clusters on densely pilose-puberulent (at times glandular) bracteolate peduncles; *involucres* campanulate, bracts biseriate, narrowly lanceolate, (3.75–)4–5 mm high, outer ones 0.5–0.75(–0.95) mm wide, green or brownish, 2-ribbed, densely pilose to nearly glabrous, apex acuminate, glandular-ciliate, at times deep red, margin entire, herbaceous to scarious, glandular-ciliate especially above; *corolla* (2.15–)2.5–3.5 mm long, funnelform, tube white, glandular to glabrous, throat blue, lilac, lavender, rarely white, the 5 lobes upright or spreading, acute, externally puberulous, pigmented as the throat; *achenes* 5-angled, black, (1.15–)1.5–1.75 mm long, scabrous on angles, carpopodium white, prominent; *pappus* of 5 free oblong, scarious scales (1.5–)2–3(–3.4) mm long, margin pectinate, apex setiferous, setae scabrous, at times the scales apically truncate and without setae, then scales 0.1–0.15 mm long.

Published cytological studies give the chromosome number $n = 10$ (Cooper & Mahoney, 1935; Turner, Ellison & King, 1961, for collections from Vera Cruz; Turner, Powell & King, 1962, for collections from Guatemala and Morelos). Morrison and Rajhathy (1960) disagree with the other authors; they report 40 chromosomes. As *Ageratum conyzoides* is tetraploid, $n = 20$, and similar in appearance to *A. houstonianum*, one wonders if Morrison and Rajhathy may have misidentified their material.

Ageratum houstonianum is closely related to *A. conyzoides* as is evidenced from the similarities of habit, achenes, pappus, corollas and the malodorous nature when fresh. The relationship is also indicated through the presence of the same alkaloid (Chevalier, 1910) and the presence of the heterocyclic compound, ageratochromene, isolated from the plants' essential oils (Alertson, 1955; Hegnauer, 1964). *Ageratum houstonianum* is often confused in herbaria, botanical gardens, and in the field with *A. conyzoides*. However, the combination of ovate leaves with cordate bases, and narrowly lanceolate, conspicuously pilose involucre bracts with stipitate glandular pubescence on the gradually acuminate apex distinguishes *A. houstonianum* from similar species.

Ageratum houstonianum is divided into formae based on characters of the pappus and involucre.

1. Pappus scales oblong, pectinate, apically setiferous, scale (1.5–)2–3(–3.4) mm long; involucre bracts stipitate-glandular, ciliate — 4a. *Ageratum houstonianum* f. *houstonianum*

1. Pappus scales oblong, pectinate, apically truncate, not setiferous, 0.1–0.15 mm long; involucre bracts with or without stipitate glands — 4b. *Ageratum houstonianum* f. *isochroum*

4a. *Ageratum houstonianum* Miller forma *houstonianum*.

- Ageratum conyzoides* Lam., Ill. Gen. Pl. Bot. 248. Pl. 672. 1823. (Holotype: op. cit. pl. 672.)
- Ageratum mexicanum* Sims, Bot. Mag. 52: 2524. 1825, fide Robinson (1913b). (Holotype: op. cit. pl. 2524; plant raised from seeds sent by Bullock from Mexico.)
- Ageratum mexicanum* Sweet, Brit. Fl. Gard. 1. t. 89. 1825, fide Robinson (1913b). (Holotype: op. cit. t. 89; plant raised from seeds sent by Bullock from Mexico.)
- Ageratum conyzoides* L. var. *mexicanum* DC., Prod. 5: 108. 1836, fide Robinson (1913b). (Holotype: based upon Sims (1825) and Sweet (1825).)
- Carelia houstoniana* (Miller) Kuntze, Rev. Gen. Pl. 1: 325. 1891, fide Robinson (1913b).
- Ageratum mexicanum* Hort. ex Vilm., Fl. Pl. Terre. Ed. 4. 43. 1894.
- Ageratum mexicanum* Hort. ex Vilm. var. *nanum* Vilm., Fl. Pl. Terre. Ed. 4. 44. 1894.
- Ageratum mexicanum* Hort. ex Vilm. var. *nanum* Vilm. forma *imperiale* Vilm., Fl. Pl. Terre. Ed. 4. 44. 1894.
- Ageratum mexicanum* Hort. ex Vilm. var. *nanum* Vilm. forma *azureum* Vilm., Fl. Pl. Terre. Ed. 4. 44. 1894.
- Ageratum mexicanum* Hort. ex Vilm. var. *nanum* Vilm. forma *multiflorum* Vilm., Fl. Pl. Terre. Ed. 4. 44. 1894.
- Ageratum wendlandii* Vilm., Fl. Pl. Terre. Ed. 4. 1894. (Holotype: unnumbered figure, op. cit., p. 2.)
- Ageratum wendlandii* Vilm. var. *albis* Vilm., Suppl. Fl. Pl. Terre. 2. 1884.
- Ageratum mexicanum* Hort. ex Vilm. forma *albiflorum* Vilm., Blumengärtnerei 2: 445. 1896.
- Ageratum mexicanum* Sims var. *majus* Vilm., Blumengärtnerei 2: 445. 1896.
- Ageratum mexicanum* Sims forma *lasseauxii* (Carr.) Vilm., Blumengärtnerei 2: 445. 1896.
- Ageratum mexicanum* Sims forma *wendlandii* Vilm., Blumengärtnerei 2: 445. 1896.
- Ageratum mexicanum* Sims var. *majus* Vilm. forma *coeruleum* Vilm., Blumengärtnerei 2: 445. 1896.
- Ageratum mexicanum* Sims var. *nanum* Vilm., Blumengärtnerei 2: 445. 1896.
- Ageratum houstonianum* Miller var. *typicum* Robins., Contr. Gray Herb. 68: 5. 1923. *Nom. inval.*
- Ageratum houstonianum* Miller var. *typicum* Robins. forma *normale* Robins., Contr. Gray Herb. 68: 5. 1923. *Nom. inval.*
- Ageratum houstonianum* Miller var. *angustatum* Robins., Contr. Gray Herb. 68: 6. 1923. (Holotype: FRANCE. Naturalized in maritime Alps, Menton, Walther s.n. (Z, not seen); tracing and small fragment, GH.)
- Ageratum houstonianum* Miller var. *typicum* Robins. forma *niveum* Robins., Contr. Gray Herb. 68: 6. 1923. (Holotype: UNITED STATES. Founded on material purchased from Joseph Breck and Sons Corporation, grown for the Department of Agriculture at Glen Echo, Maryland, Freeman 5074 (US); isotype, GH.)
- Ageratum houstonianum* Miller var. *typicum* Robins. forma *luteum* Robins., Contr. Gray Herb. 68: 6. 1923. (Holotype: UNITED STATES. Founded on material supplied by the Joseph Breck and Sons Corporation and cultivated at Glen Echo for the Department of Agriculture, Freeman 5084, in part (US); isotype, GH.)

Pappus scales apically setiferous, (1.5–)2–3(–3.4) mm long; involucre bracts narrowly lanceolate, ciliate, stipitate-glandular.

Though no type is cited by Miller (1768), his description included Houston's handwritten note "Eupatorium herbaceum melissae folio villosum flore coeruleo," which accompanied Houston's specimen collected in Vera Cruz. As it would appear that this is the only specimen upon which Miller based his description, I am designating it as the lectotype.

In his discussion, Miller states that the species "was found growing naturally at La Vera Cruz by the late Dr. William Houston." Seeds were sent to Europe and grown, the plants becoming weedy in the hot-beds of the nurseries.

Hegi (1917) states that this plant has been known in Europe since 1823, and shortly thereafter Sims (1825) described *Ageratum mexicanum* based on plants grown from seeds brought from Mexico to the Sloane Street Nursery in London by a Mr. Bullock. There is no question but that the plant Sims described and illustrated is identical to Miller's *A. houstonianum*. The ovate-deltoid, pilose, cordate-based leaf, the pubescent petiole and the red tipped phyllaries illustrated in color and described all point to the previously described species. Sweet (1825) described *A. mexicanum* basing his illustration, too, on plants grown from Bullock's seeds at the Sloane Street Nursery in London.

Candolle (1836) reduced *Ageratum mexicanum* Sims to one of four varieties under *A. conyzoides* L. The only specimen studied bearing this varietal name (microfisch, MIN) shows deltoid, cordate leaves densely pilose on the lower surface. The microfisch does not show the stem to be markedly pilose though Candolle describes it as "hirtello" (shaggy, rough). Candolle gives *A. mexicanum* of Sims and Sweet in synonymy so it is obvious that he referred to the same plant as did the earlier writers.

Ageratum houstonianum has been cultivated as an ornamental for nearly 150 years (Hegi, 1917). The variations observed in the cultivars led Vilmorin (1884, 1894, 1896) and Robinson (1923) to propose several new taxa. Both authors used height of stems and colors of the corollas as well as size and number of leaves and flowers as distinguishing characters. Vilmorin (1884, 1894) included plates of his taxa, and from these it is quite evident that he referred exclusively to *A. houstonianum sens. lat.*

Robinson's varieties and formae were described so that botanists could give "uniformity of listing when these plants are found in the wild as escapes" (Robinson, 1923). *Ageratum houstonianum* var. *typicum* and *A. houstonianum* var. *typicum* f. *normale* are names applied to plants having blue corollas and style branches. In my opinion, such names are superfluous, as this is the usual situation, and they are invalid under Art. 24 of the *Code*.

Ageratum houstonianum var. *angustatum*, described as having been found naturalized in the maritime Alps of France, suggests a garden escape. Though technical characters of the involucre, corolla, achenes, and pappus place this plant with *A. houstonianum*, the leaves are in whorls of 3 or alternate and are generally obtuse at the base. No idea of the pubescence can be gathered from the tracing (GH), though the fragment (GH) seen does suggest a general scabrous-pilose condition. Robinson's variety may well be a teratological form of the species and such should not be set apart without more data.

Ageratum conyzoides Lam. appears to be *A. houstonianum*. The plate shows ovate leaves with more or less cordate bases and a more densely pubescent stem than is commonly seen in *A. conyzoides*. Lamarck also shows the involucre bracts as narrowly lanceolate, rather than abruptly contracted apically as in *A. conyzoides*.

Due to the considerable color variations of the corolla in this species, those names applied to plants with white corollas are placed in synonymy.

This forma is native in central and southern Mexico and extends into adjacent Guatemala and British Honduras (Fig. 1), usually in damp habitats in shade or

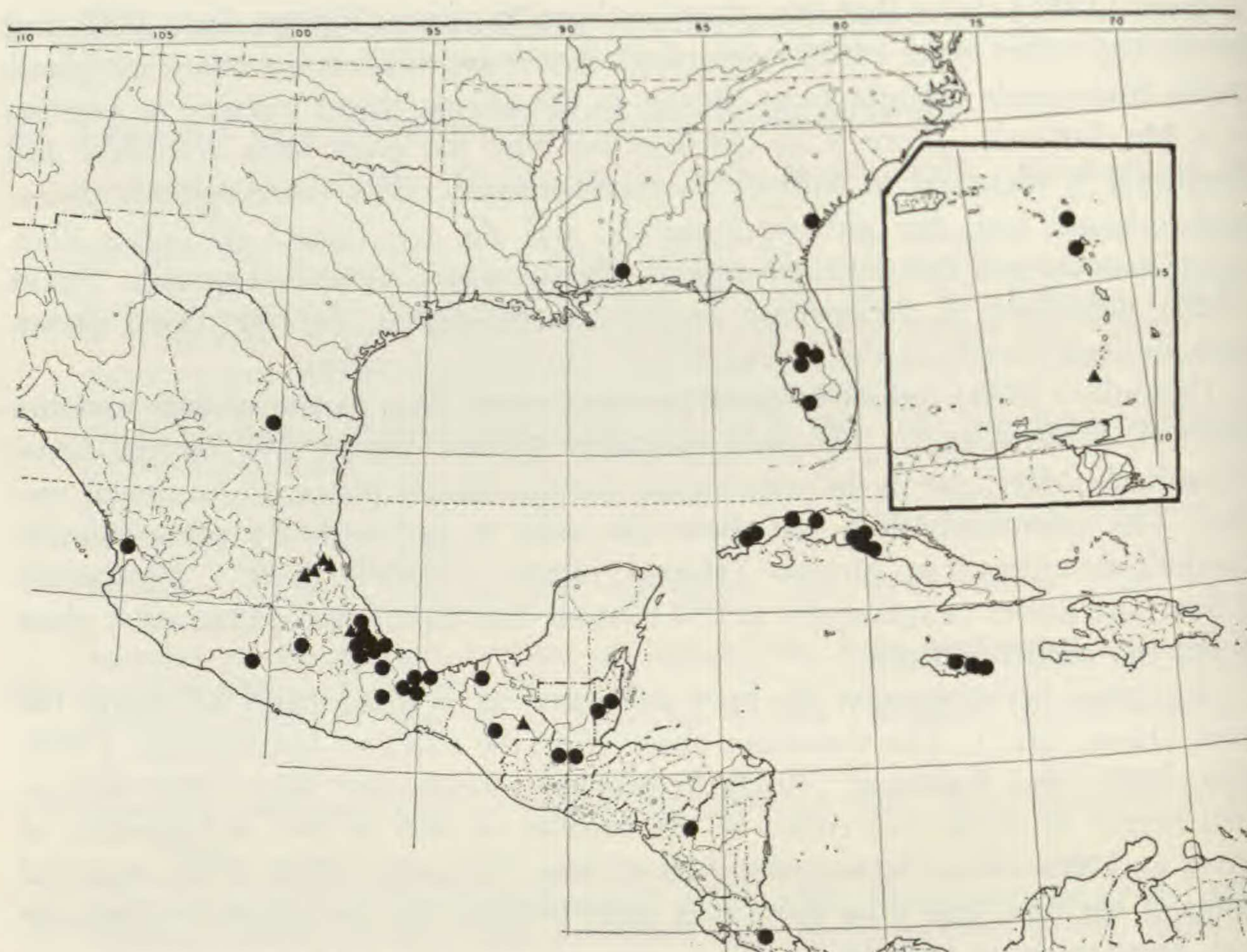


FIGURE 1. The distribution of *Ageratum houstonianum*. — Solid circle, forma *houstonianum*; triangle, forma *isochroum*. (Base map copyright University of Chicago.)

full sun from about 200–1700 m elevation, escaping from gardens and becoming established in central Florida, Cuba, Jamaica, and Hawaii. I have seen specimens from Africa, China, India, France, Java, Okinawa, the Philippines, and North Viet Nam, all of which are escapes from cultivation. The report of establishment in Alabama (Mohr, 1901) is probably based on errors in identification. Buds, flowers, and fruits are present from January through April and again from July through September but may be present throughout the year, depending on local conditions.

ANTIGUA. Liebmann 148 (GH, K, US).

BRITISH HONDURAS. El Cayo, Bartlett 12098 (GH, MICH); Gracie Rock, Sibun River, Gentle 1792 (A, K, MICH, MO, NY).

COLOMBIA. Cundinamarca, Dugand & Jaramillo 3880 (US).

CUBA. SANTA CLARA: Lomas de Banno, Ekman 16296 (A, GH, NY); San Blas, Jack 8206 (GH, NY, US).

GUATEMALA. Fields along National Route 5, ca. 4 miles S of Coban, King 3311 (MICH, NY, TEX, UC, US); ca. 2 miles W of Santa Cruz Verapaz, King 3336 (MICH, NY, TEX, UC, US); Fallabon, Lundell 2196 (MICH).

JAMAICA. Morce's Gap, Nichols 33 (F, GH, MO, NY, US).

MEXICO. CHIAPAS: Municipio de Tenejapa, Breedlove 6211 (DS, MICH); grassy swamp near Coapinala, Wonderly 28 (MICH). GUERRERO: Coyuca, Hinton 5537 (BM, GH, MO, US). MORELOS: About 11 miles S of Cuernavaca, King 4160 (F, MICH, NY, TEX, UC, US). NAYARIT: Road along river in swampy area near Tepic, Mexia 501 (A, BM, F, GH, MICH, MO, NY, UC, US). NUEVO LEON: Près Monterrey, Obbon s.n. (K). OAXACA: Yaveo, Mexia 9177 (F, GH, MO, NY, UC). TABASCO: Villahermosa, Juzepczuk 1923 (US). VERA CRUZ:

Grassy slopes among scattered shrubs, Orizaba, *Balls B4308* (K, UC, US); Vallée de Cordoba, *Bourgeau 1537* (F, GH, K, MSC, US); 5.5 miles S of Xalapa, *Johnson & Hofstetter 2004* (MIN); Jalapa, *Pringle 8065* (BM, F, GH, MIN, MSC, NY, UC, US); Mt. Orizaba, *Seaton 55* (F, GH, NY, US).

PERU. LIMA: Cascadas de Barranco, cerca de Lima, *Ferreyra 6331* (US).

Reported in Sumatra and Java (Koster, 1935), Jamaica (Fawcett & Rendle, 1936), and Madiera, Porto Santo, and Desertas (Lowe, 1868).

4b. *Ageratum houstonianum* Miller forma *isochroum* (Robins.) M. F. Johnson, comb. nov.

Ageratum houstonianum Miller var. *mutescens* Robins. forma *isochroum* Robins., Contr. Gray Herb. 68: 6. 1923. (Holotype: MEXICO. Prov. Huasteca: Wartenberg, near Tantoyuca, *Ervendberg 100* (GH); isotype, F.)

Ageratum houstonianum Miller var. *mutescens* Robins., Proc. Amer. Acad. Arts 51: 532. 1916.

Ageratum houstonianum Miller var. *mutescens* Robins. forma *versicolor* Robins., Contr. Gray Herb. 68: 6. 1923. (Holotype: Founded on material sold by the Joseph Breck and Sons Corporation and grown at Glen Echo, Maryland, for study at the Department of Agriculture at Washington, *Freeman 5084*, in part (US); isotype, GH.)

Very similar to *Ageratum houstonianum* f. *houstonianum*, differing in the presence of truncate pappus scales 0.1–0.15 mm long and the involucre bracts, which at times lack stipitate glands.

The type location as recorded on the label is inaccurate as "Prov. Huasteca" is unknown from Mexico. Smith (1899) does not include Huasteca in his index to maps, but rather Huatusco, a canton in Vera Cruz, in which the village of Tantoyuca is located. Ervendberg's collection is thus assumed to have originated in Vera Cruz.

Robinson's variety is similar to *A. houstonianum* f. *houstonianum* in leaf shape, pilose pubescence, and shape of involucre bracts, as well as having the same chromosome number, $n = 10$ (*Breedlove 9135*, MICH). However, forma *isochroum* is aberrant in two respects—general lack of gland tipped pubescence on the involucre bracts and the presence of very short pappus scales which have slightly spreading, blunt, pectinate lobes. Plants with these characters are not geographically separated from the typical members of the species; therefore the status of forma is maintained, and the available form name *isochroum* is applied.

This forma is found in Mexico, Central America, and the West Indies (Fig. 1) in habitats similar to that of forma *houstonianum*. I have seen specimens from Germany and Texas; both are garden escapes. Buds, flowers, and fruits are present as in forma *houstonianum*.

GRENADA. *Linden 1157* (MO, NY).

MEXICO. CHIAPAS: Savannah near airport of San Quintin, along the Río Jatate, *Breedlove 9135* (DS, MICH). HIDALGO: 4 miles SW of Chapulhuacan on road to Jacala, *Graham & Johnston 4732* (MICH, TEX); 12.7 miles SW of Hidalgo-San Luis Potosí state boundary, *Johnson & Hofstetter 2009* (MIN); pastured roadside sod 2.2 miles W of Santa Ana on Route 85, *Johnson & Ownbey 1960* (MIN). PUEBLA: Roadside bank 3 miles E of María Andrea, *McGregor 16463* (MSC). VERA CRUZ: C. de Tantoyuca, *Cardenas 273* (F, GH); Wartenberg, near Tantoyuca, *Ervendberg 100* (F, GH).

NICARAGUA. Moist grassy opening in a forest, Jinotega, *Grant 1307* (F, MICH).

UNITED STATES. MARYLAND: Cultivated at Glen Echo, *Freeman 5084* (GH).

5. *Ageratum conyzoides* L., Sp. Pl. 2: 839. 1753.

Type: Three specimens in the Linnaean Herbarium labeled *Ageratum conyzoides* (in Linnaeus' handwriting?) are presumably type specimens (not seen); microfisch photographs, MIN. King and Robinson (1969) have come to the same conclusion.

Annuals or sub-shrubs where growing conditions are suitable, (1.45-)2-10(-15) dm tall, malodorous when fresh; *roots* fibrous, adventitious at base if stem decumbent; *stems* erect, less commonly decumbent, branching; stems and branches reddish, becoming green above, striate, puberulous-white pilose, especially at nodes and on upper stem, to nearly glabrous; *leaves* opposite, at times alternate above, petioled, thin, ovate below, ovate to elliptic-oblong above, lower (0.7-)3-10 cm long, (0.4-)1.9-7 cm wide, upper progressively smaller, base obtuse, rarely oblique, apex acute, less commonly rounded, margin crenate, ciliate or glabrous, upper surface pilose, especially on veins, to nearly glabrous, lower surface abundantly pilose, yellow or amber glandular-punctate, less commonly nearly glabrous and eglandular-punctate; *petioles* (0.4-)1-3.3(-7.5) cm long, sparsely to abundantly white pilose, especially on upper leaves; *inflorescences* of (1-3)4-18 heads borne in terminal cymose clusters; *peduncles* bracteolate, puberulent-pilose, 0.5-1.6 cm long; *involucres* campanulate to hemispheric, bracts biseriate, oblong to lanceolate-oblong, 3-4.75(-5) mm high, outer ones 0.5-1.5(-1.75) mm wide, 2-ribbed, sparsely pilose to glabrous, green to reddish or apically and marginally tinged with red-purple, apex abruptly to less commonly gradually acuminate, puberulous, margin basally entire, apically erose to variously fimbriate, rarely entire, minutely to conspicuously ciliate-scabrate; *corolla* tubular to funnelform, 1.5-2.5(-3) mm long, glabrous to sparsely puberulent apically, tube and throat greenish to white, lobes mauve, heliotrope, blue, lavender to white, acute, erect or spreading; *achenes* 5-angled, black, 1.25-1.75(-2) mm long, scabrous on angles, carpopodium brownish or white; *pappus* of 5, rarely 6, membranous, tawny to reddish-brown oblong scales all abruptly tapering to a scabrous seta or some scales truncate, entire scale (0.4-)1.5-3 mm long in subsp. *conyzoides* or pappus 0.25-0.9 mm long, all scales oblong, apically truncate to obscurely acuminate, variously laciniate but not setiferous in subsp. *latifolium*.

The species can be divided into two subspecies based on the characters in the following key.

1. Pappus scales 1.5-3 mm long, apically tapering to a scabrous seta at least in some heads 5a. *Ageratum conyzoides* subsp. *conyzoides*
1. Pappus scales 0.25-0.9 mm long, apically truncate to obscurely acuminate, variously laciniate but not setiferous 5b. *A. conyzoides* subsp. *latifolium*

5a. *Ageratum conyzoides* L. subsp. *conyzoides*.

Ageratum hirtum Lam., Ency. Méth. 1: 53. Pl. 672, f. 2. 1783, fide Robinson (1913b). (Holotype: op. cit. Pl. 672, f. 2.)

Ageratum humile Salisb., Prod. 188. 1796.

Ageratum hirsutum Lam. in Poiret, Ency. Méth. Bot. Suppl. 1: 242. 1810, fide Robinson (1913b). (Holotype: Pl. 672, f. 2. in Lam., Illustr. 1783.)

Ageratum album Willd. ex Steud., Nomen. 18. 1821.

Cacalia mentrasto Vell., Fl. Flum. 8. t. 69. 1825, fide Baker ex Martius (1876). (Holotype: op. cit. t. 69.)

Ageratum cordifolium Roxb., Fl. Ind. 3: 415. 1832.

- Ageratum conyzoides* L. var. *hirtum* (Lam.) DC., Prod. 5: 108. 1836, fide Robinson (1913b).
- Ageratum suffruticosum* Regel, Gartenflora 3: 389. t. 108. 1854. (Holotype: op. cit. t. 108; plate of plant growing in a garden.)
- Ageratum nanum* Hort. ex Sch. Bip. in Kock & Fint., Wochenschr. 1: 26. 1858.
- Ageratum odoratum* Vilm., Fl. Pl. Terre. Ed. 2. 42. 1866, fide Robinson (1913b).
- Carelia conysodes* (L.) Kuntze, Rev. Gen. Pl. 1: 325. 1891, fide Robinson (1913b).
- Carelia conysodes* (L.) Kuntze α *robusta* Kuntze, Rev. Gen. Pl. 1: 325. 1891, fide Robinson (1913b).
- Carelia conysodes* (L.) Kuntze α *robusta* Kuntze var. *alba* Kuntze Rev. Gen. Pl. 1: 325. 1891, fide Robinson (1913b).
- Carelia conysodes* (L.) Kuntze β *umbrosa* Kuntze, Rev. Gen. Pl. 1: 325. 1891, fide Robinson (1913b).
- Carelia conysodes* (L.) Kuntze β *umbrosa* Kuntze var. *coerulea* Kuntze, Rev. Gen. Pl. 1: 325. 1891, fide Robinson (1913b).
- Carelia conysodes* (L.) Kuntze γ *pusilla* Kuntze, Rev. Gen. Pl. 1: 325. 1891, fide Robinson (1913b).
- Carelia conysodes* (L.) Kuntze γ *pusilla* Kuntze var. *alba* Kuntze, Rev. Gen. Pl. 1: 325. 1891, fide Robinson (1913b).
- Ageratum conyzoides* L. var. *inaequipaleaceum* Hieron., Bot. Jahrb. 19: 44. 1895. (Holotype: COLOMBIA. Crescit prope Papayan, Lehmann 4666 (GH); isotype, NY.)
- Ageratum conyzoides* L. forma *album* (Willd.) Robins., Contr. Gray Herb. 42: 462. 1913. (Holotype: PUERTO RICO. In graminosis ad "Cocoa," Sintenis 5874, not seen.)
- Ageratum humile* Larr., Escritos 406. 1922.
- Ageratum arsenii* Robins., Contr. Gray Herb. 64: 3. 1922. (Holotype: MEXICO. Nuevo Leon: Cercado près Monterrey, Arsène s.n. (K); sketch, GH.)

Annuals or sub-shrubs, 0.45–15 dm tall; *leaves* (0.7–)3–10 cm long, (0.4–)1.9–7 cm wide, base obtuse, rarely oblique; *petioles* (0.4–)1–3.3(–7.5) cm long; *inflorescences* terminal, the (1–)4–18 heads in cymose clusters; *peduncles* 0.5–1.5 cm long; *involucres* campanulate, bracts oblong 3–5 mm high, outer ones 0.5–1.75 mm wide, apex abruptly acuminate, margin basally entire, apically erose to variously fimbriate; *corolla* 1.5–3 mm long; *achenes* 1.25–2 mm long, scabrous; *pappus* of 5, rarely 6, membranous scales (0.4–)1.5–3 mm long, basally free and all or some abruptly tapering to a scabrous seta.

The oldest synonym is *Ageratum hirtum* Lam. (1783), a name applied to "an *Ageratum conyzoides* Lin." (Lamarck, 1783: 53). Lamarck's later name, *Ageratum hirsutum*, as represented in the plate (Lamarck, 1823), is clearly applied to *Ageratum conyzoides*.

Vellozo (1825) applied a vernacular name as the specific epithet in his *Carelia mentrasto*. The accompanying plate suggests *Ageratum conyzoides*, though the leaves are illustrated as rather thick and fleshy.

Candolle (1836) reduced Lamarck's *Ageratum hirtum* to varietal rank under *Ageratum conyzoides* L. Roxburgh (1832) described *Ageratum cordifolium* from Bengal, India. The description undoubtedly places his species with *Ageratum conyzoides*, and an *Ageratum* species collected in India must be *Ageratum conyzoides* as this is the only taxon found beyond the limits of the Western Hemisphere. Vilmorin (1866) applied the name *Ageratum odoratum* to *Ageratum conyzoides*, apparently used as garden ornamentals, giving the name *A. conyzoides* as the Latin synonym.

Kuntze (1891) removed all recognized species from *Ageratum* L. transferring them to *Carelia* Moehr. applying the rule of priority in the strictest sense. He described a series of varieties under *Carelia conysodes* (Kuntze's spelling) using

size of plants and leaves, their pubescence and corolla color as bases for his taxa. As these varieties are quite probably merely local responses to ecological conditions, they cannot be accorded taxonomic rank.

Hieronimus (1895) described *A. conyzoides* L. var. *inaequipaleaceum* to include those plants which have blunted as well as setaceous pappus scales in the same head. This character, while noticeable, is not consistent as florets bearing fully setaceous scales are often adjacent to florets with blunt scales. The plants with the aberrant pappus occupy the same geographic range as plants with a setiferous pappus; thus the status of variety cannot be maintained. Due to the inconsistent nature of this pappus character, Hieronimus' varietal name is placed in synonymy.

Ageratum arsenii Robins. (1922) is a somewhat decumbent perennial which possesses a pappus similar to that described above. These characters, which Robinson interpreted as delimiting this species, are widespread in *A. conyzoides*, and the description applies readily to this taxon. Thus the name, *A. arsenii*, must be listed in synonymy. Arsène collected the type specimen at Monterrey, Mexico, which is about 300 miles from the nearest station in Vera Cruz. It is assumed that Arsène's single collection represents a cultivar or a garden escape.

Giving taxonomic recognition to white flowered plants in this species is quite superfluous. White corollas are known to be mixed with blue ones on a single plant, the usual purplish color fades toward white with increasing age in the living plant, and the colors tend to fade on herbarium specimens so that distinguishing corolla color becomes meaningless. For these reasons, varietal and forma names alluding to white corollas are placed in synonymy.

Ageratum conyzoides subsp. *conyzoides* exhibits considerable variation, as is expected in a wide-spread taxon. Subshrubs to 10 dm tall as well as ephemeral annuals a mere 4.5 cm tall are known. These extremes indicate the plasticity of this subspecies to varying ecological conditions; tall and robust in the more optimum tropics to very dwarfed in more rigorous environments of ecological stresses. Variations in size of achenes and length of pappus, width of involucre bracts and length and width of leaves is also evident. Those specimens from South America, in many instances, possess structures at the upper limits of the size range. Plants from the Philippine Islands are quite consistent in having involucre bracts at the lower end of the size range. Pubescence on the South American plants is often longer than the pubescence of plants from other areas. Other examples of size variation are not as sharply restricted geographically and are more difficult to cite. In all cases, however, the plants possess the key features of *A. conyzoides* subsp. *conyzoides*, and it is most desirable to treat this widespread subspecies as in the past, *i.e.*, as one variable taxon.

Ageratum conyzoides subsp. *conyzoides* is a tetraploid, $2n = 40$ (Turner & King, 1964; Turner & Lewis, 1965; Powell & King, 1969; Löve, 1966) which may account in part, for its widespread weediness (*cf.* Baker, 1965). The tetraploidy is consistent over the wide geographic range from which chromosome counts are known. The only published chromosome number indicating otherwise is that of Ishikawa (1916) and Mehra *et al.* (1966) in which the number $n = 10$ is recorded. As no voucher for this number is given in either paper, one cannot

ascertain if a correct determination of the authors' material was made and if this number applies here.

Ageratum conyzoides subsp. *conyzoides* is distinguished from *A. conyzoides* subsp. *latifolium* by the characters listed in the key to subspecies and by the different ploidy levels of these taxa. *Ageratum conyzoides sens. lat.* is similar to *A. houstonianum sens. lat.* but is readily distinguished as discussed under the latter species.

This subspecies is native in South and Central America (Fig. 2); adventive and common as a pantropic weed extending about 20° north and south of the equator from sea level to *ca.* 2500 m elevation (Fig. 3). It is reported from southeastern United States (Chapman, 1883); these are records of cultivars. Flowers and fruits are present during the entire year, depending somewhat on location and local conditions.

ANTIGUA. Tyrells, *Box 1122* (US).

ARGENTINA. 25 km E of Jujuy, Río Zapala, *Eyerdam & Beatle 22370* (GH, MO, UC).

AUSTRALIA. QUEENSLAND: Rock Hampton, *Russell, Jr. s.n.* (UC).

BAHAMA ISLANDS. Eleuthera, *E. G. Britton 6375* (F, NY, US).

BELGIAN CONGO. [Republic of the Congo.] Catuba, *Quarro 3217* (MO).

BOLIVIA. Yucachaca, *Steinbach 9680* (GH, MO, NY, UC).

BRAZIL. Vicosia, *Mexia 4718* (GH, K, MO, NY, UC); Itapiranga, *Smith & Reitz 12629* (GH, MO, WIS).

BURMA. Haka, *Dickason 7711* (A).

CAMEROON. Without locality, *Braun 14* (NY).

CHILE. Santiago, *Claude-Joseph 1604* (US).

CHINA. Yeung Ling shan, *Lau 183* (GH, MICH, MO, NY, UC); Shiu Chau, *To et al. 97L* (UC).

COLOMBIA. Bucaramanga, *Fassett 25587* (MICH, WIS); SE of Quetame, *Pennell 1796* (GH, NY).

COSTA RICA. Cartago, *Cooper 5824* (NY, US).

DOMINICA. Without locality, *Cooper 77* (GH, MICH, MO, NY, UC, US).

DOMINICAN REPUBLIC. Loma Bajita, *Valeur 922* (K, MO, NY, US).

ECUADOR. Canyon of the Río Chanchan, near Huigra, *Camp E-3161* (GH, K, MO, NY, UC, US); Banos, *Landeman 4* (BM, K); Galápagos Islands, Indefatigable Island, *Stevenson 212* (UC).

EGYPT. Lougier, *Kralik s.n.* (DS, GH).

EL SALVADOR. Volcan de San Salvador, *Standley 22871* (GH, US).

FORMOSA. Tomita-cho, Taihoku-shi, *Tanaka & Shimada 11194* (MICH, MO, NY, UC).

GUATEMALA. Gualan, *Deam 330* (GH, MICH, MO, NY, US); Santa Rosa, *Heyde & Lux 3781* (F, GH, NY, US); between Escuintla and Santa Lucia Cotz, *Standley 63459* (F).

BRITISH GUIANA. Moruka River, Pomeroon District, *de la Cruz 2545* (GH, MO, NY, US).

FRENCH GUIANA. Cayene, *Broadway 20* (GH, NY, US).

HAITI. Pennery, *Ekman 2490* (A, US).

HONDURAS. Vicinity of El Zamorano, *Standley 24646* (F, GH, NY, US); along Río Choluteca at Ojo de Agua, *Williams 17312* (F); vicinity of La Ceiba, *Yunker et al. 8239* (F, GH, K, MICH, MO, NY, US).

INDIA. Barapani, Khasi Hills, *Koelz 22968* (MICH).

KENYA. 8 miles NE of Runyerjes, cytological voucher, *Lewis 5912* (MO, TEX).

LAOS. Chochinchina, *Gandoger s.n.* (MO).

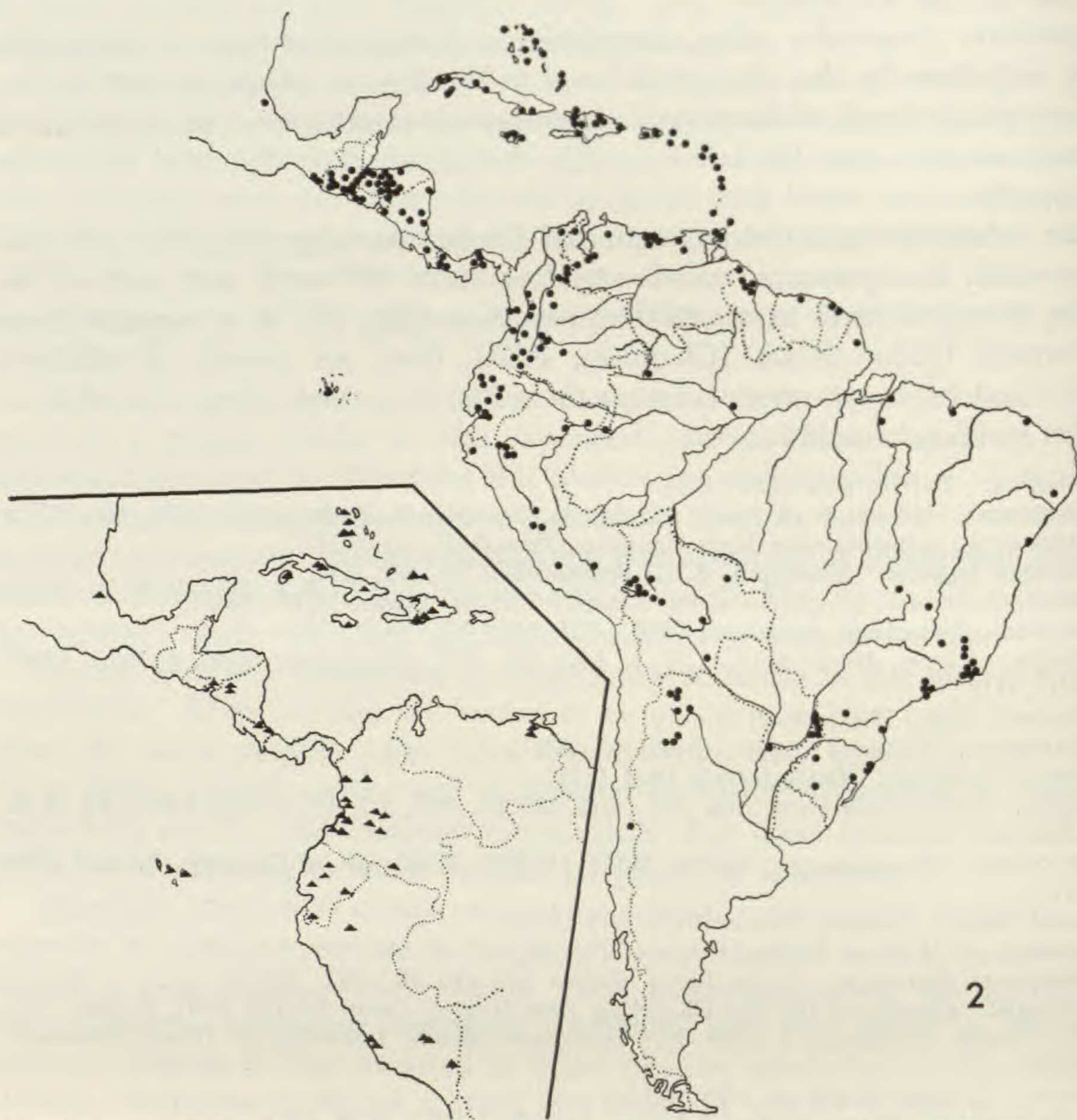
LIBERIA. 3 miles NE of Suacoco, Gbarnga, *Okeke 12* (MO, UC).

MEXICO. CHIAPAS: Tapachula,, *Fischer 35427* (F). NAYARIT: Tepic, *Palmer 1850* (F, GH). PUEBLA: 6 miles SW of Puebla-Vera Cruz state border, *King 4140* (F). VERA CRUZ: Chontla, C. de Tantoyuca, *Cardenas 433* (F).

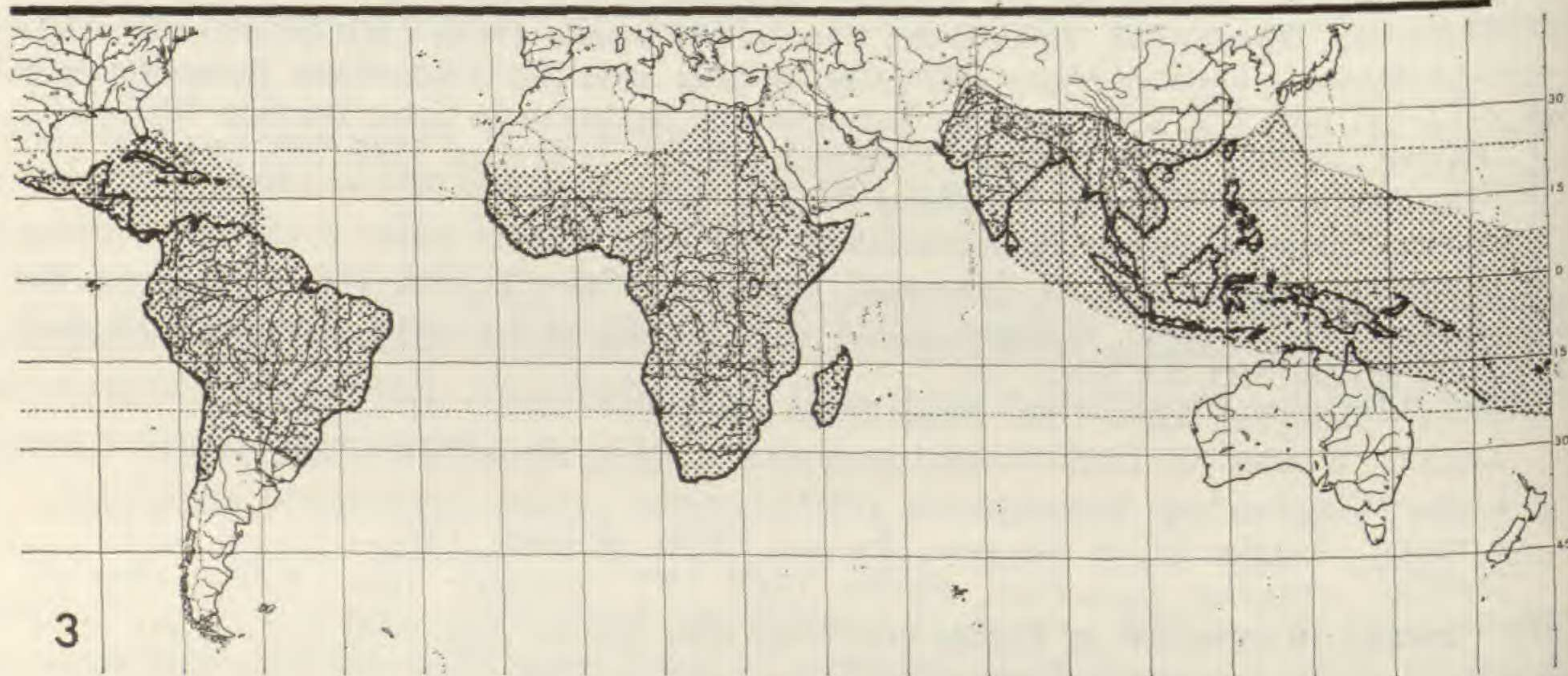
MOZAMBIQUE. Sabi River, Merinqua district, *Chase 2595* (NY).

NEPAL. 6 miles N of Hitaura, *Brydon 29* (DS).

NICARAGUA. Chinandego, *Baker 2021* (GH, K, MO, MSC, NY, UC, US); Cerro Sialci, sierra SW of Jinotega, *Standley 10598* (F).



2



3

FIGURES 2-3. — 2. The distribution of *Ageratum conyzoides* in the New World. Solid circle, subsp. *conyzoides*; triangle, subsp. *latifolium*. — 3. The pantropical distribution of *Ageratum conyzoides subsp. conyzoides*.

- NIGERIA. Baba Eko, Ijebu Prov., *Ross* 297 (MO, NY).
 NORTHERN RHODESIA. [Zambia.] Kitwe, Ndola district, *Linley* 162 (MO).
 PANAMA. Concepción, cytological voucher, *King* 5286 (TEX, UC, US); El Valle, cytological voucher, *King* 5327 (TEX, UC, US).
 PERU. Zepalacio, *Klug* 3470 (GH, MO, NY, US).
 PHILIPPINE ISLANDS. Manila, *Merrill* 35 (GH, MO, NY).
 PUERTO RICO. 2 miles W of Ponce, *Heller* 6143 (GH, MO, NY, US); Gaguas, *Mills-paugh* 208 (NY).
 RUANDA. Minuli, *Troupin* II 639 (MIN, MO).
 ST. CROIX. *Ricksecker* 430 (DS, GH, MIN, MO, NY, UC, US).
 SINGAPORE. Bord des routes, Singapore, *Debeaux* s.n. (NY).
 SOUTH AFRICA. Durban, *Schlechter* 2934 (MO).
 SOUTHERN RHODESIA. [Rhodesia.] Belingew, *West* 2772 (MO).
 SUDAN. Katire, *Jackson* 381 (MO).
 SURINAM. Paramaribo, *Samuels* 192 (GH, NY).
 TANGANYIKA. [Tanzania.] 4 miles W of Tanga, *Lewis* 6060 (MO, TEX).
 THAILAND. 11 km S of Khas Yai Forest Station and 105 km E of Saraburi, cytological voucher, *King* 5537 (GH, TEX, UC); 16 km NNE of Ranong, cytological voucher, *King* 5577 (TEX, UC).
 UNITED STATES. HAWAII: Kawaihapai, *Degener* 11034 (GH, MICH, MO, NY, WIS).
 VENEZUELA. Tovar, *Pittier* 9362 (GH, NY, US).
 UGANDA. Mabira Forest, *Loveridge* 19 (A, MO).
 VIET NAM. Tourane, *Clemens* 3082 (MICH, MO, MSC, NY, UC).

5b. *Ageratum conyzoides* L. subsp. *latifolium* (Cav.) M. F. Johnson, comb. et stat. nov.

- Ageratum latifolium* Cav., Ic. 4. t. 357. 1797. (Holotype: PERU: Prope Liman, *Nee* s.n. (MA, not seen); photograph, MIN.)
Ageratum brachystephanum Regel, Gartenflora 3: 245. tab. 108, fig. c. 1854, fide Robinson (1913b). (Holotype: op. cit. tab. 108, fig. c.)
Ageratum muticum Griseb., Fl. Brit. W. Ind. 356. 1861, fide Robinson (1913b).
Ageratum maritimum Sch. Bip. ex Griseb., Fl. Brit. W. Ind. 356. 1861, non HBK (1820), fide Robinson (1913b).
Calea densiflora Klatt, Leopoldina 20: 96. 1884, fide Robinson (1913b).
Carelia brachystephana (Regel) Kuntze, Rev. Gen. 1: 325. 1891, fide Robinson (1913b).
Carelia mutica (Griseb.) Kuntze, Rev. Gen. 1: 325. 1891, fide Robinson (1913b).

Annuals, 2–8 dm tall; *leaves* ovate, (1.5–)3–6.5(–7.4) cm long, 2–5(–5.7) cm wide, base obtuse to truncate, rarely cordate; *petioles* 0.8–3 cm long; *inflorescences* terminal, 3–12 heads grouped in corymbose clusters; *peduncles* 0.5–1.6 cm long; *involucres* hemispheric to less commonly campanulate, bracts lanceolate-oblong, 3.5–5 mm high, outer ones (0.5–)0.65–1.4(–1.5) mm wide, apex gradually or abruptly tapering to a scabrous apex, margin entire or variously erose to fimbriate apically; *corollas* 1.5–2.5 mm long; *achenes* (1.25–)1.5–1.85(–2) mm long, scabrous; *pappus* of 5 free membranous, oblong, tawny scales 0.25–0.7 mm long, margin entire to variously erose, apex truncate to obscurely acuminate, not setiferous.

The synonym *Ageratum brachystephanum* Regel (1854) is clearly a name applied to this taxon as is evidenced from the figure, labeled *A. brachystephanum*, of an achene with a pappus of short scales accompanying the plate of *A. suffruticosum* Regel (Regel, 1854). *Ageratum muticum* Griseb. (1861) was the name applied to this subspecies in the West Indies and referred to plants with some setiferous pappus scales in each inflorescence. *Ageratum maritimum* Sch. Bip. ex Griseb. (1861) non HBK (1820) was applied to plants of the West Indies and Peru which possessed a pappus of free, awnless scales. The description in

Grisebach (1861) indicates that Schultze's name is a synonym for the older *A. latifolium* Cav. Klatt's description of *Calea densiflora* (1884) indicates that his name is synonymous with *A. conyzoides* subsp. *latifolium*. Kuntze's names under *Carelia*, fall automatically into synonymy. See the discussion under *A. conyzoides* subsp. *conyzoides* as well. *Ageratum latifolium* Cav. var. *galapageium* Robins. (Robinson, 1913b) possesses achenes which lack a pappus and should be referred to the epappose genus *Alomia*.

Cavanilles (1797), when he described *Ageratum latifolium*, was well aware of the similarities between it and *A. conyzoides*. He went to considerable length to point out that *A. conyzoides* has pappus scales drawn out apically into a long seta and that his species was notably different because its pappus scales are always short and without setae. After studying numerous specimens of *A. latifolium*, it is evident to me that the pappus character is not sufficient to separate *A. latifolium* from *A. conyzoides*. The pappus of *A. conyzoides* subsp. *conyzoides* has, at times, setiferous scales as well as truncated ones on the same fruit. The distinguishing feature of both species as conceived by earlier authors is combined in one head, or even one flower.

Other morphological characters which are of high taxonomic value elsewhere in this genus are of little value in distinguishing *Ageratum conyzoides* and *A. latifolium* as separate species. The involucral bracts are the same size, shape, and of the same texture; the bract margins are similarly erose or fimbriate. Achenes and corollas are identical in both taxa. Leaves are of the same shape and texture in both taxa, though those of subsp. *latifolium* tend to be slightly shorter and wider at the base than in subsp. *conyzoides*. Pollen grains have been studied in both taxa. The grains are extremely similar in size and wall sculpture, though subsp. *latifolium* tends to have grains with echinae slightly longer than grains of subsp. *conyzoides*. However, this is not a consistent feature and cannot be used as a taxonomic character. Studies of plastic peels showing guard cells from the lower leaf surface revealed no characters of taxonomic merit.

An apparently consistent morphological character distinguishing these subspecies is present only in the pappus scales as given in the key—non-setiferous ones in subsp. *latifolium* versus at least some setiferous scales in subsp. *conyzoides*. This feature, in combination with diploidy, $2n = 20$ in subsp. *latifolium* (Turner, Powell & King, 1962), and tetraploidy, $2n = 40$ in subsp. *conyzoides* (Turner & King, 1964; Turner & Lewis, 1965; Löve, 1966; Powell & King, 1969), serves to distinguish these otherwise very similar taxa.

Though the taxa considered here have been recognized as species for nearly 200 years, I have reduced them to subspecies under the older name *A. conyzoides* L. The reduction cannot be carried further because the difference in ploidy level quite certainly hinders gene exchange between them. Any hybrid progeny would be triploid and, if viable, probably sterile. Thus the designation of subspecies.

Ageratum conyzoides subsp. *latifolium* is native in western South America and Central America, occurring in moist grasslands and on mountain slopes and in forests, less commonly as a weed in waste places and villages, from sea level to ca. 2500 m elevation (Fig. 2). It is in flower and fruit during the entire year, but most commonly from November through April.

BAHAMA ISLANDS. Little Harbor Cay, *Britton & Millspaugh* 2240 (F, NY, US).

COLOMBIA. Near Río San Joaquin, *Killip* 7812 (GH, NY, US); Villavicencio, *Pennell* 1597 (GH, NY); Bogotá, *Triana* 1157 (BM, NY, P, US).

COSTA RICA. Potrero at Pejivalle Farm, above Río Pejivalle, *Dodge & Thomas* 4336 (GH, MO, US).

CUBA. Vedado, *Baker* 1411 (F, NY).

DOMINICAN REPUBLIC. Paradis, *Fuertes* 458 (NY, US).

ECUADOR. Cumbaco, *Mille* 532 (GH, K, MO, NY, US); Galápagos Islands, San Cristobal, *Schimpff* 147 (BM, MO, NY, P).

HAITI. Vicinity of Mission, Fonds Varettes, *Leonard* 3644 (GH, NY, US).

HONDURAS. San Juan del Rancho, N of Cerro de Uyuca, *Standley* 15149 (F).

JAMAICA. Peckham, Upper Clarendon, *Harris* 12825 (BM, GH, NY).

MEXICO. HIDALGO: 12 miles SW of Hidalgo-San Luis Potosí state border, cytological voucher, *King* 4226 (F, MICH, NY, TEX, UC). NAYARIT: 9 miles N of Compostela, *McVaugh & Koelz* 556 (MICH).

NICARAGUA. Jinotega, *Grant* 7307 (GH).

PERU. 40 km S of Lima, *Grant* 7503 (GH); 2–6 km from Oconeque, *Metcalf* 30601 (GH, MO, UC, US).

VENEZUELA. Between La Sabana de las Piedras and Cerro Negro, *Steiermark* 61833 (US).

6. *Ageratum gaumeri* Robins., Proc. Amer. Acad. Arts 47: 191. 1911.

Holotype: MEXICO. Yucatan: Izamal, *Gaumer* 395 (GH); isotypes, DS, K, MICH, MO, NY, P, UC, US.

Annual, 1.5–4 dm tall; *roots* fibrous, rarely adventitious at basal nodes; *stem* erect, abundantly branched, generally pilose at nodes, internodes sparsely pilose to glabrous; *leaves opposite* or rarely alternate above, thin, ovate to less commonly deltoid, (0.6–)2.3–6.5(–8) cm long, (0.3–)1.6–4.1(–6.4) cm wide, base obtuse, apex acute, margin crenate-dentate, sparsely strigose, upper surface pale green to brown, smooth, sparingly pilose to glabrous, lower surface similar, venation inconspicuous; *petioles* 1–3(–3.5) cm long, pilose or glabrous; *inflorescences* borne singly on glabrous to sparingly pilose bracteolate peduncles (2.1–)4.5–13.5(–15) cm long; *involucre*s campanulate, bracts biseriata, lanceolate, 2–3 mm high, 0.4–0.75(–1) mm wide, prominently 2-ribbed, glabrous to sparsely pilose, green to rose-colored apically, margin scarious, entire to slightly erose to scabrous, apex gradually to abruptly acuminate; *corollas* funnelform, 1.3–2.2 mm long, tube pale green to white, glabrous, the 5 lobes blue, lilac or lavender, glabrous to marginally puberulent; *achenes* brown, (1.1–)1.25–1.7 mm long, sparsely scabrous on angles, slightly curved toward the oblique white carpopodium; *pappus* of 5 white or rose-colored, membranaceous, blunt scales (0.05–)1.05–1.8(–2.05) mm long, apex variously fimbriate, at times finely setiferous or minute and coroniform.

Ageratum gaumeri may be divided into formae based on characters of the pappus and tomentum of the leaves.

- | | |
|---|--|
| 1. Pappus of 5 scales; leaves pilose | 6a. <i>Ageratum gaumeri</i> forma <i>gaumeri</i> |
| 1. Pappus coroniform, minute; leaves generally glabrous | 6b. <i>Ageratum gaumeri</i> forma <i>fallax</i> |

6a. *Ageratum gaumeri* Robins. forma *gaumeri*.

Ageratum intermedium sensu Millspaugh, Field Columbian Mus. Publ. Bot. Ser. 3: 90. 1904, non Hemsley (1887), fide Robinson (1913b).

Leaves sparingly pilose; pappus of scales 0.35–1.85(–2.05) mm long.

The original *Ageratum gaumeri*, which is included in this forma, was distributed as *A. corymbosum* Zuccag. and *A. intermedium* Hemsley. This forma

is readily distinguished from *A. corymbosum* by its annual habit, its ovate, thin leaves, its pappus of laciniate to setiferous scales and its inflorescences of a single head; from *A. intermedium* (i.e., *A. maritimum* HBK) by its inflorescences, pappus, thin leaves, more numerous bracts on the peduncle and upright habit. The long bracteolate peduncle bearing a single head is the most constant characteristic of *A. gaumeri* and serves to set it apart from all other taxa.

This forma occurs in Yucatan and northern Guatemala at 15–30 m elevation. Buds, flowers, and mature fruits are generally present from December through March (occasionally in May, June, August).

GUATEMALA. PETEN: Arroyo (Río) Petexbatum S of Sayaxcho, *Steiermark* 46184 (F, MICH); Sayaxche, *Steiermark* 46252 (F).

MEXICO. YUCATAN: Izamal, *Armour* 72 (F), *Coulter* 72 (F); Valladolid, *Crockett* 86 (MICH); Izamal, *Gaumer* 395 (BM, DS, GH, K, MICH, MO, NY, P, UC, US); San Anselmo, *Gaumer* 1735 (BM, F, GH, MO, US); Chichankanab, *Gaumer* 2508 (F), *Gaumer s.n.* (F, K); Xnococ, *Gaumer & Sons* 23482 (BM, GH, K, MO, NY, US); Izamal, *Greenman* 374 (F); Chichen Itza, *Goldman* 564 (F, US), *Lundell & Lundell* 7859 (MICH), *Steere* 1009 (GH, MICH, US); Merida, *Schott* 208 (F); without locality, *Valdez* 13 (F, GH, MICH, MO, NY, US); without locality or collector, 3925 (F, GH).

6b. *Ageratum gaumeri* Robins. forma *fallax* Robins., Contr. Gray Herb. 104: 4. 1934.

Holotype: MEXICO. Yucatan: Muna, *Steere* 2125 (GH); isotype (MICH).

Leaves glabrous; pappus coroniform, minute, 0.05–0.1 mm long, margin undulate.

Robinson (1934) described *Ageratum gaumeri* f. *fallax* as distinct because the achenes possess a very minute coroniform pappus which, in association with the more glabrous leaves, set this taxon apart.

Forma *fallax* occurs in Yucatan and on Cozumel Island. Flowers and fruits are present in July and August.

MEXICO. QUINTANA ROO: Savannah N of Lake Coba, *Lundell & Lundell* 7782 (MICH); low forest, San Miguel, Cozumel Island, *Steere* 2633 (GH, MICH). YUCATAN: Hills S of Muna, along roadside, *Lundell & Lundell* 8172 (GH, MICH, US); Muna, on rocks, on high ridge, *Steere* 2125 (GH, MICH).

Section II. *Coelestina* (Cass.) Gray, Syn. Fl. 1(2): 93. 1884.

Coelestina Cass., Bull. Soc. Philom. Par. 1817: 10. 1817.

Caelestina Cass., Dict. Sci. Nat. 16: 10. 1820.

Coelestinia Endl., Gen. 366. 1838.

Ageratum subgenus *Coelestina* (Cass.) Baker in Mart., Fl. Bras. 6(2): 197. 1876.

Woody or herbaceous *perennials*; roots fibrous, or rarely a taproot; leaves opposite, lanceolate, ovate, deltoid, elliptic or linear, variously pubescent and glandular-tomentose to glabrous; *inflorescences* grouped in tight or loose corymbiform clusters or borne in an irregular panicle; *involucral bracts* 2-seriate, lanceolate, linear-lanceolate, apex gradually acuminate, acute or rounded, margin entire, glabrous or ciliate; *receptacles* naked or paleaceous; *corollas* tubular to funnelform, varying shades of lavender and blue to white; *achenes* glabrous; *carpopodium* conspicuous; *pappus* coroniform, rarely bearing marginal subulate setae.

Lectotype: *Ageratum corymbosum* Zuccag.

Species in this section are found in the pine-oak forest zones of Mexico and extend through Central America to Panama; less common occurrences are in extreme southern Florida and the West Indies. Flowering and fruiting occur, in the main, from June through January; local conditions may favor year around blooming.

KEY TO SPECIES IN SECTION *COELESTINA*

1. Heads not clustered, borne in an irregular panicle; plants generally glabrous throughout; leaves lanceolate, sessile or very short petioled; British Guiana 26. *Ageratum scorpioideum*
1. Heads in an open or tight corymbiform cluster; plants with tomentum and glandular-atoms; leaves ovate, deltoid, elliptic or lanceolate; petioles evident; widespread in Mexico, Central America, and South America 2
2. Receptacles of all heads paleaceous 3
3. Heads small, the involucre bracts (3.0–)3.25–4 mm long 4
4. Paleae linear, firm, indurate apically; Mexico 5
5. Leaves thin, ovate to lanceolate, 5.5–9.5 cm long, 2.4–3.6 cm wide, both surfaces glabrous or puberulous over the venation, lower surface conspicuously glandular-atomiferous 12. *Ageratum elassocarpum*
5. Leaves more or less firm, lanceolate, (2.4–)5–12(–12.5) cm long, (1.4–)3.3–5 cm wide, both surfaces white pilose to densely so beneath, lower surface glandular-atomiferous 11. *Ageratum nelsonii*
4. Paleae spatulate, lax, erose apically; Brazil 10. *Ageratum micropappum*
3. Heads larger, involucre bracts 4–5(–6) mm long 6
6. Leaves deltoid, rarely ovate, base truncate, lower surface densely white woolly, eglandular; root a taproot 15b. *Ageratum tomentosum* f. *bracteatum*
6. Leaves ovate, elliptic, lanceolate to linear, base cuneate, lower surface white pilose, glandular-atomiferous; roots fibrous 7
7. Leaves ovate to elliptic 8
8. Lower leaf surface conspicuously covered with amber to yellow-colored glandular-atoms; corolla lobes violet, glandular-atomiferous; pappus 0.2–0.5 mm high; flowering in October, rarely earlier 8. *Ageratum paleaceum*
8. Lower leaf surface with few, if any, yellow glandular-atoms; corolla lobes white, eglandular; pappus 0.4–0.5(–0.7) mm high; flowering in July and August 7. *Ageratum albidum*
7. Leaves lanceolate to linear 9. *Ageratum echinoides*
2. Receptacles of all heads naked or paleae few and sporadic in a single head 9
9. Perennial herbs, stems decumbent to repent, rarely erect; leaves succulent or thin; plants of seashore habitat 10
10. Pappus coroniform but deeply laciniate; leaves succulent, ovate, borne on petioles 0.3–1(–2) mm long; stems, petioles, and peduncles sparingly white pilose 19. *Ageratum maritimum*
10. Pappus coroniform, margin entire or at times setiferous, but not deeply laciniate; leaves thin, ovate or deltoid, borne on petioles 1–3.6 cm long; stems, petioles, and peduncles glabrous to very sparingly tomentose 20. *Ageratum littorale*
9. Shrubs, stems woody, erect, only very rarely decumbent at the base; leaves not succulent, but if thin, plants not of seashore habitat 11
11. Heads large, (0.6–)0.8–1 cm in diameter; leaves shiny on both surfaces, upper bright green and orange glandular punctate, lower surface pale green, densely glandular punctate 25. *Ageratum lucidum*
11. Heads small, not greater than 5 mm in diameter; both leaf surfaces never shiny or only the upper surface shiny 12
12. Involucre bracts lanceolate (0.85–)1–1.35 mm wide, glabrous to sparingly pilose, margin entire, ciliate at least apically, to glabrous 13

13. Leaves ovate, 4–9.5 cm long, 3–6 cm wide, upper surface yellow-green, margin crenate, venation on the lower surface conspicuous, often red; petioles slightly winged; involucral bracts green to reddish, 5.25–6.5 mm long, (0.85–)1–1.35 mm wide, prominently 2-ribbed basally 21. *Ageratum platypodum*
13. Leaves lanceolate, 1.1–8 cm long, 0.7–2.9 cm wide, upper surface bright green, margin sharply dentate, venation inconspicuous, not red; petioles not winged; involucral bracts green to reddish, 4.2–6.85 mm long, (0.7–)1–1.3 mm wide, 2-ribbed, the ribs conspicuous 22. *Ageratum riparium*
12. Involucral bracts lanceolate to linear-lanceolate, less than 1 mm wide, more abundantly pilose, rarely glabrous, margin entire, glabrous, rarely ciliate apically 14
14. Leaves remote from the inflorescences, somewhat thick, fleshy and velvety; stems white pilose, hairs *ca.* 0.75 mm long 18. *Ageratum guatemalense*
14. Leaves not conspicuously remote from the inflorescences, not thick, fleshy and velvety; stem, if pilose, with shorter hairs 15
15. Leaves thin, semi-membranous, borne on elongate petioles 16
16. Leaves broadly ovate, 7–9 cm long, 6.5–9 cm wide, upper surface bright green, lower surface pale green, abundantly dotted with yellow glandular atoms; venation palmate, conspicuous, pilose; petioles 2.5–4 cm long, white pilose, narrowly winged; involucral bracts pale brownish to pale green, glabrous 23. *Ageratum oerstedii*
16. Leaves narrowly ovate, 3–6.6 cm long, 1.4–4.15 cm wide, upper surface shiny green, lower surface dull, gray to off-green, less conspicuously dotted with glandular atoms; venation reticulate, conspicuous, sparingly pilose; petioles 1.2–3 cm long, pilose-puberulous, not winged; involucral bracts pale green to reddish, pilose basally 24. *Ageratum petiolatum*
15. Leaves not semi-membranous, petioles not elongate 17
17. Leaves rigid, lanceolate to ovate, margin entire, lower surface densely covered with pale gray to silvery indument 18
18. Leaves lanceolate, (3.5–)4–6 cm long, *ca.* 1.7 cm wide, upper surface scabrous to scabrous-puberulent, eglandular-punctate, lower surface densely white-tomentose, eglandular; petioles 0.7–0.8 cm long; involucral bracts 4.75–5 mm long, 0.55–0.6 mm wide, dark green, white pilose and eglandular throughout 17. *Ageratum chortianum*
18. Leaves ovate, 2–3.5 cm long, 1–2 cm wide, upper surface scabrous to puberulent, amber glandular-punctate, lower surface densely white to gray tomentose with scattered amber glandular-atoms; petioles 0.1–0.4 cm long; involucral bracts 3.5–4.5 mm long, 0.5–0.65 mm wide, green to deep reddish, puberulous and glandular-atomiferous 16. *Ageratum standleyi*
17. Leaves not rigid, ovate, lanceolate, elliptic or deltoid, margin crenate or dentate, at times remotely so, not entire, lower surface variously covered with white pubescence or scabrous 19
19. Leaves deltoid, rarely lanceolate, 1.6–3.5(–6.5) cm long, lower surface densely white tomentose; plants shrubby, small, to 4.5 dm tall; root a taproot 15a. *Ageratum tomentosum* f. *tomentosum*

19. Leaves not deltoid, larger than above, lower surface pilose to scabrous; plants shrubby, larger, to 24 dm tall; roots fibrous 20
20. Leaves ovate, upper surface conspicuously dark green or brown, lower surface abundantly white tomentose at least over the prominent primary venation; involucre bracts conspicuously pilose; extreme southern Mexico and Central America, rare northward 14. *Ageratum rugosum*
20. Leaves ovate, ovate-lanceolate, triangular-lanceolate, narrowly lanceolate or elliptic-lanceolate, upper surface green, at times shiny green but not conspicuously dark green or brown, lower surface densely to sparingly pilose or scabrous, primary venation conspicuous and white or inconspicuous; involucre bracts pilose, rarely densely so; common in Mexico 13. *Ageratum corymbosum*

7. *Ageratum albidum* (DC.) Hemsl., Biol. Centr. Amer. Bot. 2: 81. 1881.

Coelestina albida DC., Prod. 5: 107. 1836. (Holotype: MEXICO. Oaxaca: Inter Oaxaca et Mitla, Andrieux 548 (DC-G, not seen), photograph, MIN; isotype, K, photographs, F, GH, US, fide Robinson (1913b).)

Carelia albida (DC.) Kuntze, Rev. Gen. 1: 325. 1891, fide Robinson (1913b).

Herbs 4–6.5 dm tall from perennial roots; *roots* fibrous, woody, coarse; *stems* erect, simple, branching only near summit, herbaceous and reddish, becoming woody and gray toward base, puberulent-pilose throughout to glabrous basally; *leaves* opposite, petioled, thickened, ovate to elliptic, (2.7–)3–5(–6.9) cm long, 1.2–2.5(–3.5) cm long, base obtuse to cuneate, margin crenate, revolute, scabrous, apex widely acute, upper surface dark green, more or less rugulose, conspicuously white, long pilose and scabrous, lower surface paler green, densely long, white pilose to less densely covered, at times, with scattered yellow glanduliferous atoms, the 3–5 veins white, prominent; *petioles* 1–4 mm long, densely white pilose; *inflorescences* terminal, the 5–20 heads in a convex corymbose cluster; *peduncles* less than 5 mm long, densely white puberulous-pilose, bracteolate; *bracteoles* linear, green, puberulous and pilose, about 3 mm long; *involucre* campanulate, bracts bi- or tri-seriate, firm, 2-ribbed, green, apically white or reddish, lanceolate, 4–5(–5.5) mm high, outer ones 0.8–0.9(–1) mm wide, margin entire, green or scarious, at times ciliate, apex acute, surface white pilose; *receptacle* paleaceous, paleae firm, linear, 4–5(–5.2) mm long, apex acute, white; *corollas* narrowly funnelform, 2.25–3 mm long, white throughout, tube and throat white-pilose, lobes glabrous; *achenes* black, (1.35–)1.5–2.25 mm long, glabrous, slightly tapered toward white carpodium; *pappus* coroniform, 0.4–0.5(–0.7) mm long, margin undulate, irregular.

Ageratum albidum is related to *A. paleaceum* as evidenced from similar receptacle paleae and general morphology in both. However, the species are readily separable as indicated in Table 2. From this summary, it is evident that though these species may be sympatric in at least part of their ranges, reproductive isolation operating through different blooming times may maintain their distinctness.

TABLE 2. A comparison of *Ageratum albidum* and *A. paleaceum*.

Character	<i>A. albidum</i>	<i>A. paleaceum</i>
Corolla color.	White.	Violet.
Glands.	Few to none.	Numerous amber to yellow atomiferous glands on the lower leaf surfaces, peduncles, bracteoles, and corollas.
Growth habit.	Perennial herbs.	Woody, perennial shrubs.
Flowering and fruiting.	July to September.	October to December.

Ageratum albidum is distinguished from *A. elassocarpum*, another paleaceous species, by the lavender corollas, the more glabrous leaves, shorter pappus, and a more southern distribution of the latter species.

Robinson (1913b) described *Ageratum albidum* (DC.) Hemsl. var. *nelsonii* based on *Nelson 2822a* (GH). In the description, he states that this variety is similar in involucre, paleae, pappus, etc. to *A. albidum*, differing in wider leaves on longer petioles and a more leafy stem. Comparisons of morphological measurements of leaves, involucral bracts, paleae, and pappus quickly shows these taxa to be quite different as summarized in Table 3.

It is my opinion that the plants previously determined as *Ageratum albidum* var. *nelsonii* cannot be treated in this way. The combination of characters found in these plants, densely pilose leaves on long petioles and small heads with receptacle paleae, is found nowhere else in the genus. Thus it is more logical to treat these plants as a separate species, *Ageratum nelsonii* (Robins.) M. F. Johnson.

Ageratum albidum occurs locally in Oaxaca, Mexico, in open sun in association with oaks and leguminous shrubs in rocky clay-loam soil from ca. 1700–2500 m elevation. Flowers are present in July and August; fruits are present in September and dispersed in October.

MEXICO. OAXACA: Valley of Etla, *Alvarez 751* (GH); between Oaxaca and Milta, *Andrieux 548* (K); steep slope with *Quercus* and *Pinus* 3 km E of Istlan de Juarez, *Breedlove 12225* (MICH); Cerro de San Felipe, *Conzatti & Gonzales 542* (GH); vicinity of Cerro Zempoaltepetl, near Tlahuitoltepec, *Hallberg 955* (MICH, US); ruins of Monte Alban, *Johnson*

TABLE 3. A comparison of *Ageratum albidum* and *A. nelsonii*.

Character	<i>A. albidum</i>	<i>A. nelsonii</i>
Leaves.	Ovate to elliptic, 2.7–6.9 cm long, 1.2–3.5 cm wide.	Lanceolate, 2.4–12.5 cm long, (1.4–)3.3–4 cm wide.
Petioles.	1–4 mm long.	(0.2–)1–2.5 cm long.
Involucre.	4–5.5 mm high, outer bracts 0.8–0.9(–1) mm wide.	3.25–4 mm high, outer bracts 0.5–0.85(–1) mm wide.
Paleae.	4–5.2 mm high.	3.3–3.75 mm high.
Pappus.	0.4–0.5(–0.7) mm high.	(0.1–)0.15–0.3 mm high.

& Hofstetter 1997 (MIN), Kenoyer 1523 (GH), King 3490 (DS, MICH, NY, TEX, UC, US); mountains along route 175 ca. 24 miles N of the junction with route 190, King 3502 (TEX); valley of Oaxaca, Nelson 1208 (GH, US); hills above Oaxaca, Pringle 4816 (BM, F, GH, K, MICH, MIN, MO, MSC, NY, P, UC, US); Monte Alban, C. L. Smith 365 (MO, UC, US); Las Sedas, C. L. Smith 366 (F, NY); Tenango, L. C. Smith 424 (GH).

8. *Ageratum paleaceum* (DC.) Hemsl., Biol. Centr. Amer. Bot. 2: 83. 1881.

Coelestina paleacea Gay ex DC., Prod. 5: 107. 1836. (Holotype: MEXICO. Oaxaca: Circa Oaxaca, Andrieux 287 (DC-G, not seen), photographs, GH, US; isotype, P. fide Robinson (1913b).)

Carelia paleacea (DC.) Kuntze, Rev. Gen. 1: 325. 1891, fide Robinson (1913b).

Ageratum rhytidophyllum Robins., Proc. Amer. Acad. Arts 36: 476. 1901. (Holotype: MEXICO. Oaxaca: Sierra de San Filipe, Pringle 5675 (GH), photograph, MIN.)

Perennial shrubs 4–7.5(–12) dm tall; roots fibrous; stems erect, simple or branched from an enlarged woody caudex, younger parts deep red, puberulous-tomentose to pilose, densely so toward inflorescences, older parts brownish-gray, puberulous-tomentose to glabrous; leaves opposite, petioled, thickened, lower ones ovate, 3.9–5.7(–6) cm long, 1–2 cm wide, upper ones ovate-lanceolate to lanceolate, base of blade obtuse, rarely oblique, apex acute, margin revolute, very shallowly crenate to entire, upper surface dull to bright green, at times partially purple or bluish, rugose, scabrous, lower surface pale green, conspicuously reticulate-veined, densely covered with white pilose hairs and amber or yellow atomiferous glands; petioles 0.3–0.6(–0.9) cm long, puberulous-tomentose to pilose with scattered yellow or amber atomiferous glands; inflorescences terminal, the 20–30 or more heads grouped into dense corymbose clusters; peduncles coarse, bracteolate, usually less than 5 mm long, puberulous with scattered yellow or amber and/or black atomiferous glands; bracteoles alternate, less than 3 mm long, green to tawny, puberulous-tomentose with scattered atomiferous glands, merging with involucre bracts; involucre campanulate, bracts triseriate, more or less firm, lanceolate to linear, inner bracts 4–5(–6) mm long, 0.5–0.8 mm wide, outer bracts about one half as long, green to purple, white pilose to sparingly so, 2-ribbed, margin entire, at times ciliate and/or scarious, apex acute, slightly thickened, white; receptacle paleaceous, paleae linear, 3.25–5 mm long, pale green to purplish, apex acute, white, minutely scabrous; corollas funnelform, 2.2–3(–3.2) mm long, sparingly puberulous and glandular-atomiferous on tube or at least on lobes to glabrous, tube and narrow throat pale green, the 5 acute lobes and exerted style branches violet to pale violet; achenes 5-angled, shiny brown to black, 1.4–1.9(–2.25) mm long, glabrous, tapering toward small carpodium; pappus coroniform, whitish, 0.2–0.3 mm high, margin entire or obscurely dentate.

Ageratum paleaceum (DC.) Hemsl. was described by Candolle (1836) based upon C. Gay's unpublished, but proposed, name for Andrieux 287. It was placed in the genus *Coelestina* Cass. and transferred to *Ageratum* by Hemsley (1881). Robinson (1901) was apparently unaware of Gay's earlier name when *A. rhytidophyllum* was published. This oversight was corrected in Robinson's revision of 1913.

Ageratum paleaceum is similar to *A. albidum* but is readily distinguished from it and other species by the short-petioled, thick, ovate leaves which are

white pilose and conspicuously dotted with orange glanduliferous atoms beneath. See discussion under *A. albidum* as well.

The chromosome number $n = 11 \pm 1$ reported by Turner, Powell & King (1962) for "*Ageratum* cf. *paleaceum* (Gay) Hemsl. var. *paleaceum*" is taken from King 3112. Personal study of this specimen indicates it cannot be referred to *A. paleaceum* but rather to *A. elassocarpum*.

This species occurs in Oaxaca, Michoacán, and Puebla from ca. 1500–2800 m elevation. Buds and flowers are present in October, rarely before; fruits are present in November and December.

MEXICO. MICHOACAN: 1 km S of Jacona, Cutler 4058 (US). OAXACA: 3 km E of Ixtlan de Juros, Breedlove 12230 (MICH); Ixtlan de Juarez, Krueger & Gillespi 2 (GH, MO); valley of Oaxaca, Nelson 1439 (US); Nelson 1446 (GH, US); Sierra de San Felipe, Pringle 5675 (GH); Pringle 6177 (F, GH, MIN, MO, MSC, NY, P, UC, US); Cerro Verde, Purpus 4424 (UC); Cerro Espino, Reko 3538 (US); Las Sedas, C. L. Smith 364 (NY, UC); Sierra de San Felipe, C. L. Smith 594 (F, MO, UC, US); San Juan del Estado, L. C. Smith 277 (GH). PUEBLA: Moria, Nicolas s.n. (F).

9. *Ageratum echioides* (Less.) Hemsl., Biol. Centr. Amer. Bot. 2: 81. 1881.

Isocarpha echioides Less., Linnaea 5: 141. t. 2, fig. 14–16. 1830. (Holotype: MEXICO. Vera Cruz: In graminosis prope Hacienda de la Laguna, Schiede 304 (B, not seen), photograph, GH.

Carelia echioides (Less.) Kuntze, Rev. Gen. 1: 325. 1891.

Alomia echioides (Less.) Robins., Contr. Gray Herb. 42: 449. 1913.

Perennial herbs 3.5–6.5 dm tall from a gnarled woody caudex; roots coarse, fibrous; stems erect, simple to sparingly branched near summit, leafy on lower half, upper half naked or with 1 or 2 pairs of reduced leaves, surface deep red to tan, densely white pilose-puberulent basally and toward midregion to nearly glabrous, pilose hairs up to 0.1 mm long; leaves opposite, somewhat firm, elliptic-lanceolate to nearly linear, 5–7.5(–13.5) cm long, 0.8–1.5(–2.6) cm wide, base long attenuate-cuneate, apex acute to broadly so, margin revolute, scabrous, remotely and shallowly crenate, upper surface dull, dark green, white pilose to scabrous, pubescent over the 3 longitudinal veins, lower surface pale green, yellow glandular-punctate, white pilose, at times densely so over the 3 prominent white veins, to glabrous; petioles ca. 0.2–1.2 cm long, slightly winged, densely white pilose to glabrous; inflorescences terminal, the 5–11 or more heads grouped in tight corymbose clusters; peduncles less than 5 mm long, puberulous to pilose-puberulous; involucre campanulate, bracts triseriate, lanceolate-oblong, 4–4.5(–5) mm high, 0.65–1.05 mm wide, green, becoming red apically, surface with scattered pilose hairs, prominently 2-ribbed basally, margin herbaceous to scarious, entire, pilose, apex acute, white, subindurate; corollas tubular to narrowly funnel-form, 2.2–2.75 mm long, tube and throat pale green, short pilose to glabrous, lobes acute, erect or spreading, pale blue to bluish-purple, sparingly pilose to glabrous; receptacle conical, paleaceous, paleae light green, apically red, linear to spatulate, 3.75–5 mm long, 0.3–0.5 mm wide, 1-ribbed, margin entire, at times scarious, apex acute, indurate, white, minutely scabrous; achenes black (1.35–) 1.45–1.8 mm long, glabrous, basally tipped with inconspicuous carpodium; pappus coroniform, tawny, 0.05–0.25(–0.55) mm high, margin dentate to variously coarsely pectinate.

The type specimen of *Ageratum echiodides* is quite probably not extant as the collection of Compositae held at Berlin (B) was destroyed during World War II. At least, I was unable to find the type when I visited Berlin in 1966.

Robinson (1913*b*) and Candolle (1836) recognized this species as belonging with the epappose genus *Alomia* HBK. However, the plants at hand do possess a coroniform pappus, though in certain instances a very small one, and thus are here referred to section *Coelestina* of *Ageratum*. I have seen some specimens Robinson annotated as *Alomia echiodides*, and even these show the pappus.

This species appears most closely related to *Ageratum guatemalense*. See the discussion under that species. *Ageratum echiodides* also resembles *A. ellipticum* in general habit, leaf shape and size, pubescence, and in the corollas which are glabrous or nearly so. These species differ markedly in the pappus, setiferous scales in *A. ellipticum* and coroniform in *A. echiodides*. The presence of receptacle paleae in *A. echiodides* also serves to distinguish these species. *Ageratum echiodides* is similar to the paleaceous species *A. albidum* in size and shape of corollas, achenes, and involucral bracts but differs in the bluish corollas, shorter pappus and the distinctive elliptic-lanceolate to linear, tri-veined, somewhat firm leaves generally borne on the lower half of the stem. These characters separate *A. echiodides* from other paleaceous species as well.

Ageratum echiodides is found in eastern and southern Mexico and adjacent Guatemala in association with *Quercus* and *Pinus* and in moist pastures and fields and on slopes from *ca.* 1600–1950 m elevation. Flowering occurs in June–August and September, less commonly later; fruits are mature and dispersed in October.

GUATEMALA. Near Jacaltenango, Nelson 3561*a* (US); between Guatemala and San Raimundo, Standley 62978 (MICH); below Miramar, Steyermark 51500 (F, GH, NY).

MEXICO. CHIAPAS: Steep slope along road to Mal Paso, Breedlove 10343 (MICH); pasture at NW edge of Teopisca along Mexican Highway 190, Breedlove 10533 (MICH); 4 miles N of Jitotol on road to Pueblo Nuevo Solistahuacan, Breedlove 12057 (MICH); 17 miles E of La Trinitaria along road to the Lagos de Montebello, Breedlove & Raven 13028 (MICH); between Mazapa and Motozintla, Matuda 4867 (MO); Comitán, Matuda 15798 (F); *ca.* 13 miles SE of San Cristobal de las Casas, Ownbey & Muggli 3986 (MIN). GUERRERO: Acapulco, Hancock 36 (F). JALISCO: Guadalajara, Holway 511 (NY). VERA CRUZ: Orizaba, Botteri 408 (BM), Botteri 623 (GH); region d'Orizaba, Bourgeau 2393 (GH, P); region of San Andreas Tuxtla, Dressler & Jones 251 (GH, US); between Fortín and Coscomatepec, Langman 3614 (US); Zacuapan, Purpus 1854 (MO), Purpus 2199 (F, GH, US); without definite location, Bourgeau 3207 (GH, P), Sartorius s.n. (GH).

10. *Ageratum micropappum* Baker in Mart., Fl. Bras. 6(2): 198. 1876.

Holotype: BRAZIL. Bahia Province, Blanchet 3700 (K, not seen); isotypes, C, GH, P; photographs, GH, TEX, P, US.

Shrub, height unknown; *roots* unknown; *stem* conspicuously ribbed longitudinally, deep red to brown, white puberulent with scattered yellow glandular atoms, becoming tomentose near inflorescences; *leaves* opposite, petioled, subcoriaceous, ovate to lanceolate, 6–7.8 cm long, 2.9–3.8 cm wide, base cuneate, slightly decurrent along petiole, apex broadly rounded, margin slightly revolute, dentate, teeth thickened, cuspidate, upper surface glabrous or with widely scattered yellow glandular atoms, the reticulate venation inconspicuous, lower surface conspicuously white to tan tomentose with yellow glanduliferous atoms over

surface and prominent reticulate veins; *petioles* winged, *ca.* 0.7–1.5 cm long, tomentose and glandular atomiferous beneath, glabrous above; *inflorescences* terminal, heads grouped into a dense corymbose cluster; *peduncles* white-tomentose, glandular atomiferous, bracteolate; *bracteoles* linear, tomentose; *involucres* campanulate, bracts biseriate, firm, 2-ribbed, oblong, *ca.* 3.25 mm long, *ca.* 0.8–0.85 mm wide, margin entire, ciliate toward apex, apex rounded, variously ciliate or erose; *receptacle* paleaceous, paleae flattened, spatulate to lanceolate, *ca.* 4–4.25 mm long, 0.5–0.65 mm wide, 2-ribbed, margin entire, glabrous to sparingly ciliate, apex rounded, obtuse, ciliate or more or less erose; *corollas* narrowly funnelform, *ca.* 2–2.25 mm long, tube and throat white, glandular to glabrous, lobes glabrous, lavender (?); *achenes* black, 1.85–2.05 mm long, glabrous, slightly tapered toward white carpopodium; *pappus* coroniform, 0.1–0.15 mm high, margin undulate to minutely dentate.

Ageratum micropappum is distinguished by the oblong, ciliate, 2-ribbed receptacle paleae, the involucral bracts with rounded apices, the firm, ovate leaves with cuspidate teeth, the lower surfaces of the leaves with dense tomentum and the prominent, reticulate venation. Only one other species of *Ageratum* is present in Brazil, the weedy *A. conyzoides* with which *A. micropappum* cannot be confused.

This species is known only from the type locality. Flowering and fruiting data are not known.

BRAZIL. BAHIA: *Blanchet* 3700 (C, GH, P); Mt. Taboa, Boanfin, *Curran* 201 (GH, US).

11. *Ageratum nelsonii* (Robins.) M. F. Johnson, stat. et comb. nov.

Ageratum albidum (DC.) Hemsl. var. *nelsonii* Robins., Contr. Gray Herb. 42: 471. 1913. (Holotype: MEXICO. Chiapas: Between Zanatepec and Tapaná, *Nelson* 2822a (GH), photograph, MIN.)

Perennials, 4–5 dm tall; *roots* fibrous, coarse, from a woody caudex; *stem* erect, woody, simple or branched, bark brown to deep red, pilose-puberulent to densely white pilose; *leaves* opposite, petioled, lanceolate, (2.4–)5–12(–12.5) cm long, (1.4–)3.3–5 cm wide, base obtuse, apex acute, margin revolute, crenate or dentate, scabrous, upper surface dull dark green to brownish green, at times mixed with deep red, abundantly white pilose to scabrous, venation reticulate, inconspicuous, lower surface pale green, yellow to amber glandular atomiferous, densely white pilose, at times becoming so dense as to obscure surface, venation reticulate, the 3 principal veins prominent; *petioles* (0.2–)1–2.5 cm long, white scabrous as well as pilose; *inflorescences* terminal, the 20 or more heads grouped in a tight, convex corymbiform cluster; *peduncles* *ca.* 5–7 mm long, white pilose and amber glandular atomiferous, at times densely pilose, bracteolate; *bracteoles* alternate, subulate, white pilose, green to reddish; *involucres* campanulate, bracts biseriate, lanceolate, 3.25–4 mm long, outer ones 0.5–0.85(–1) mm wide, 2-ribbed though at times obscurely so, surface green, white pilose and at times glandular atomiferous, margin entire, green to scarious, at times apically ciliate, apex acute, becoming white and more or less indurate; *receptacle* conical, paleaceous, paleae linear, 3.3–3.75 mm long, 1-ribbed, pilose to glabrous, green to reddish, becoming white and indurate apically, margin entire, apex acute; *corollas* funnelform,

2–2.5(–2.75) mm long, tube and narrow throat white to pale blue or lavender, glabrous to sparingly dotted with yellow glandular atoms, lobes acute, blue to lavender, glabrous; *achenes* dull black, (1.15–)1.3–1.55 mm long, slightly tapered toward white carpopodium; *pappus* coroniform, (0.1–)0.15–0.3 mm high, margin 5-dentate or merely undulate.

Ageratum nelsonii was first described as a variety of *A. albidum* as noted in the discussion of the latter. However, the pilose stem and involucre bracts, and the larger densely pilose leaves suggest affinities elsewhere. The relatively large, pilose leaves with dark green upper surfaces are similar to leaves of *A. rugosum* from which it can be distinguished by means of the paleaceous receptacles, smaller heads and short pappus. Receptacle paleae borne in small heads and the presence of lanceolate leaves on elongate petioles suggest an affinity with *A. elassocarpum*. However, the glabrous to nearly glabrous leaves of *A. elassocarpum* and the densely pilose ones of *A. nelsonii* serve well to distinguish these species. The combination of lanceolate, rather densely pilose leaves on elongate petioles, receptacle paleae and small heads are features unique to *A. nelsonii*.

Turner, Powell & King (1962) published the chromosome number $n = 10$ for *King* 2981 which was reported as *Ageratum* cf. *tomentosum* (Benth.) Hemsl. and for *King* 2751 which was reported as *A. paleaceum* (Gay) Hemsl. var. *nelsonii* Rob. Personal study of these vouchers indicates beyond question that they should be referred to *A. nelsonii* and the number, $n = 10$, to this species.

Ageratum nelsonii occurs in the states of Mexico, Oaxaca, and Chiapas in association with *Pinus* and *Quercus* in rocky, gravelly soil from near sea level to ca. 2000 m elevation. It flowers from June to September (–October); fruits are present from July to December.

MEXICO. CHIAPAS: 1 km NW of Aguacatenango, *Breedlove* 7891 (DS, MICH); 11 miles S of La Trinitaria, *Breedlove* & *Raven* 13269 (MICH); 2 miles S of Tuxtla Gutierrez, *Breedlove* & *Raven* 13349 (MICH); 15 miles SE of Tapanatepec, *Breedlove* & *Raven* 13722 (MICH); 7 miles E of the Chiapas-Oaxaca border, *King* 2751 (MICH, TEX); 10 miles E of the Chiapas-Oaxaca border, cytological voucher, *King* 2981 (MICH, TEX); Monserrate, *Purpus* 10233 (GH, US), *Purpus* 9104 (F, GH, MO, NY, US). MEXICO: Tlalpam, *Rose* & *Hay* 5496 (US). OAXACA: Mountains about Yalalag, *Nelson* 971 (US); between Zanatepec and Tapan, *Nelson* 2821 (US), *Nelson* 2822a (GH).

12. *Ageratum elassocarpum* Blake, Contr. U. S. Natl. Herb. 22: 588. 1924.

Holotype: MEXICO. Chiapas: Sierra de Tonala, *Purpus* 6628 (US); isotypes, B, BM, F, MO, NY, UC. Type distributed as *Ageratum corymbosum* Zuccag.

Perennial *shrubs* (2–)4–7 dm tall; *roots* fibrous; *stems* erect to lax above, branched, herbaceous above, woody below, bark reddish on young stems to, at times, gray-brown on older parts, densely white puberulous over-all to glabrous toward base; *leaves* thin, opposite, rarely alternate above, petioled, ovate to lanceolate above, 5.5–9.5 cm long, 2.4–3.6 cm wide, base cuneate, apex acute to broadly so, margin shallowly crenate to subentire, upper surface dark green, puberulous to scabrous, lower surface green, glabrous to puberulous over veins, conspicuously (15× magnification) glandular-atomiferous, glands shiny to dull yellow or amber, at times mixed with black atoms; *petioles* (0.5–)1–1.8 cm long, channeled adaxially, puberulous-tomentose; *inflorescences* terminal, 12–20 or

more heads grouped in dense corymbose clusters; *peduncles* ca. 5 mm long, bracteolate, densely puberulous with scattered yellow, amber or rarely black glandular atoms; *bracteoles* alternate, green, ca. 2–3 mm long, puberulous-glandular atomiferous over both surfaces; *involucres* campanulate, bracts biseriate, firm, 2-ribbed, lanceolate, 2–3.75(–4) mm high, outer ones 0.5–0.75(–0.85) mm wide, green throughout to tinged with red, apically white, surface white puberulous with scattered yellow or black atomiferous glands, margin entire, apex acute, minutely scabrous; *receptacle* paleaceous, paleae linear, 2–2.75 mm long, firm, pale green below to apically white, glabrous to scabrous-ciliate, glandular-atomiferous apically, margin entire, apex acute; *corollas* tubular to narrowly funnelform, (1.5–)2–2.25 mm long, glabrous to minutely puberulous with scattered yellow or black atomiferous glands, tube and throat pale green to white, the 5 acute lobes and exerted style branches blue to bluish-lavender; *achenes* 5-angled, dull black, 1.25–1.5(–1.8) mm long, glabrous, tapering toward white carpopodium; *pappus* coroniform, 0.2–0.3 cm high, light tan, margin denticulate, projections extending ca. 0.05 mm above the ribs of the achene.

Ageratum elassocarpum shows affinities with *A. corymbosum* sens. lat. and especially to forma *elachycarpum* in leaf shape and size, overall external morphology, and habitat preference. Both *A. elassocarpum* and *A. corymbosum* f. *elachycarpum* have small heads with involucral bracts less than 4 mm high. The pappus is 2–3 mm high in both taxa which is shorter than in the bulk of *A. corymbosum* sens. lat. Though often determined as *A. paleaceum* or *A. corymbosum*, *A. elassocarpum* is distinct from similar species and formae. The combination of small heads with receptacle paleae and thin ovate-lanceolate leaves that are quite glabrous on the lower surface serves well to separate this species from those with which it may be confused.

The chromosome number $n = 11 \pm 1$, voucher *King 3112* (DS, MICH, NY, TEX, UC, US), was reported for *Ageratum* cf. *paleaceum* (Gay) Hemsl. var. *paleaceum* by Turner, Powell & King (1962). From study of this voucher I am convinced that *King 3112* should be referred to *A. elassocarpum* as it has the thin ovate-lanceolate nearly glabrous leaves and small heads associated with *A. elassocarpum* and never found on *A. paleaceum*. The collection of the voucher in Chiapas also indicates that it cannot be *A. paleaceum* as the range of the latter is farther north.

This species is restricted to Chiapas and adjacent Oaxaca in association with *Quercus* and *Pinus*, in full sun or partial shade ca. 500–1960 m elevation. It flowers from late June through October; fruits are present in September and mainly dispersed by December.

MEXICO. CHIAPAS: Pan-American Highway, 23 miles W of Ocozocautla, *Cronquist 9680* (MICH, MO, MSC, NY, TEX, US); low hills along route 195, about 36 miles S of Tuxtla Gutierrez, *King 3107* (DS, MICH, NY, TEX, UC, US); 22 miles S of Las Cruces, cytological voucher, *King 3112* (DS, MICH, NY, TEX, UC, US); Sierra de Tonala, *Purpus 6628* (BM, F, MO, NY, UC, US); steep, moist roadside slope covered with *Pinus* and grasses, 19 km N of Arriaga on highway 195, *Roe et al. 862* (WIS). OAXACA: Grazed areas 28 km NW of La Ventosa along the Trans-Isthmian highway, *King 632* (MICH, US); grazed areas 2 km E of Zanatepec, *King 1953* (MICH, NY, TEX, UC, US).

13. *Ageratum corymbosum* Zuccag. ex Pers., Syn. 2: 420. 1807, non Benth. (1852).

Neotype: MEXICO. Jalisco: 4.5 miles W of Tizapan on S shore of Laguna de Chapala, Johnson & Hofstetter 1981 (MIN).

Shrubs to sub-shrubs (1.5–)3.5–20 dm tall; *roots* fibrous, coarse, rarely adventitious on lower stem; *stems* woody, erect and usually clumped from a woody caudex, simple or branched, bark deep red to purplish distally, becoming brown to gray toward base, pilose-puberulent throughout to short puberulent toward inflorescences to nearly glabrous on older parts, rarely rhizomatous; *leaves* opposite, at times alternate near inflorescences, petioled, extremely variable in dimensions and shape (see key to formae below), base cuneate to truncate, margin revolute, crenate to dentate to shallowly lobed to subentire, scabrous to pilose, apex acute, upper surface smooth, dull green, scabrous to scabrous-puberulous to sericeous, lower surface dull, pale green, dotted with yellow to amber glanduliferous atoms, abundantly white pilose to puberulous at least over the reticulate venation; *petioles* variable in length (see below), channelled axially, puberulent-pilose; *inflorescences* terminal on stems and branches, the numerous heads grouped into dense or less commonly open corymbiform clusters; *peduncles* 0.5–4 cm long, white pilose-puberulous, bracteolate; *bracteoles* (2.5–)3–4.5 mm long, subulate, green to red-purple, white puberulous to velutinous; *involucre*s campanulate to hemispherical, bracts firm, biseriate, greenish to apically red, 2-ribbed, linear-lanceolate to lanceolate, (2–)2.75–7 mm high, outer ones 0.45–1(–1.1) mm wide, margin entire, herbaceous or scarious, at times ciliate apically, apex acute, reddish, minutely scabrous, submucronate, surface white pilose, at times densely so, at times dotted with yellow or amber glanduliferous atoms; *receptacle* naked or rarely 1 head of plant sparingly paleaceous; *corollas* narrowly funnelform, (1.75–)2–3.75(–4.25) mm long, tube greenish to white, short pilose, throat white, pilose, yellow or amber atomiferous to subglabrous, lobes acute, spreading, short pilose to glabrous, blue to bluish, gray-blue, lavender-purple, mauve or white; *achenes* 5-angled, dark brown to black, glabrous, (1.1–)1.3–3(–3.5) mm long, slightly tapered toward inconspicuous basal carpodium; *pappus* coroniform, white to tawny, 0.2–0.85 mm high, margin entire to lobed to variously finely pectinate, at times setiferous, setae subulate, firm, connate basally, entire pappus then 1.1–3.2 mm long.

Zuccagni (ex Persoon, 1807) did not cite any specimens, and citations of specimens are lacking in the list of synonyms as well. Thus I have chosen a personal collection as neotype, as I feel it best exemplifies the taxon as originally described.

This variable species is separated into formae based on the following key characters.

1. Involucral bracts (2.05–)2.4–3.5(–4) mm high, achenes 1.2–1.65(–1.75) mm long, leaves ovate to lanceolate; Guatemala and Honduras, rarely Mexico 13f. *A. corymbosum* f. *elachycarpum*
1. Involucral bracts higher and achenes longer, leaves widely ovate, ovate-lanceolate, triangular-lanceolate, narrowly lanceolate, elliptic-lanceolate; widespread in Mexico 2
2. Leaves narrowly lanceolate, 3.3–10 cm long, 0.5–1.8(–2.4) cm wide, margin sub-entire to remotely crenate-dentate 13b. *A. corymbosum* f. *salicifolium*

2. Leaves not narrowly lanceolate or if so, the margin grossly and coarsely dentate to lobed, not sub-entire 3
3. Leaves elliptic-lanceolate, 4.2–8.5 cm long, 1.5–3.3 cm wide, margin coarsely and conspicuously crenate-dentate, teeth at times becoming large and lobe-like, upper surface bright, shiny green, rarely dull green, venation reticulate, white and conspicuous on both surfaces 13c. *A. corymbosum* f. *lactiflorum*
3. Leaves not elliptic-lanceolate, margin not lobed, upper surface usually dull green, venation not conspicuous at least on the upper surface 4
4. Leaves ovate to ovate-lanceolate, 4–7 cm long, (1.5–)2–3.5 cm wide, margin crenate to dentate, upper surface scabrous to pilose, lower surface sparingly white pilose to scabrous; abundant in Mexico 13a. *A. corymbosum* f. *corymbosum*
4. Leaves ovate to widely so, to triangular-lanceolate, margin crenate to dentate, upper surface pilose to scabrous, lower surface densely pilose 5
5. Leaves ovate to triangular-lanceolate, 4.5–8(–11.3) cm long, 2.3–4.5 (–5.9) cm wide, margin crenate to dentate to subentire, petioles to 2.6 cm long 13d. *A. corymbosum* f. *albiflorum*
5. Leaves widely ovate, (3–)4.2–7 cm long, (1.5–)3–4.5 cm wide, margin crenate to less commonly dentate, teeth coarse, petioles shorter 13e. *A. corymbosum* f. *euryphyllum*

13a. *Ageratum corymbosum* Zuccag. ex Pers. forma *corymbosum*.

Sparganophorus ageratoides Lag., Elench. Hort. Matr. 25. 1815, fide Robinson (1913b).
Ageratum coelestinum Sims, Bot. Mag. t. 1730. 1815, fide Robinson (1913b). (Holotype: loc. cit. t. 1730.)

Coelestina coerulea Cass., Dict. 6. Suppl. 8. 1817, fide Robinson (1913b).

Coelestina corymbosa (Zuccag.) DC., Prod. 5: 108. 1836, fide Robinson (1913b).

Coelestina suffruticosa Sweet, Hort. Brit. 229. 1826, fide Robinson (1913b).

Coelestinia lessingiana Klotzsch ex Walp., Rep. 2: 545. 1843, fide Robinson (1913b).

Coelestinia lessingiana (Klotzsch) Hemsl., Biol. Cent. Amer. Bot. 2: 81. 1881, fide Robinson (1913b).

Carelia corymbosa (Zuccag.) Kuntze, Rev. Gen. 1: 325. 1891, fide Robinson (1913b).

Ageratum corymbosum Zuccag. forma *album* Robins., Contr. Gray Herb. 42: 475. 1913. (Holotype: MEXICO. Jalisco: Near Huejuquilla, Rose 2538 (GH); isotype, US; photograph, MIN.)

Coelestina sclerophylla Wooton & Standl., Contr. U. S. Natl. Herb. 16: 176. 1913. (Holotype: MEXICO. Sonora: Guadalupe Canyon, Merton 2031 (US).)

Shrubs to 20 dm tall; *leaves* ovate to ovate-lanceolate, 4–7 cm long, (1.5–)2–3.5 cm wide, base obtuse, apex acute, margin revolute, scabrous, crenate to dentate, upper surface shiny to dull green, scabrous, lower surface pale green, sparingly white pilose to scabrous, dotted with yellow to amber glanduliferous atoms; *inflorescences* grouped in flat-topped, congested corymbiform clusters; *involucral bracts* 2-ribbed, narrowly lanceolate, 4.5–6.5 mm long, 0.5–0.8 mm wide, margin entire, green to scarious, apex acute, white pilose and at times dotted with glanduliferous atoms; *corollas* tubular to narrowly funnelform, 2.5–3.5 mm long, tube and narrow throat pale green to white, pilose and/or glandular atomiferous, lobes acute, pilose to glabrous, blue, lavender, mauve to white; *achenes* (1.6–)2–2.6 mm long, dark brown to black, slightly tapered toward inconspicuous white carpodium; pappus coroniform, 0.25–0.6(–0.7) mm high, margin finely and variously fimbriate to dentate, rarely, if ever, setiferous.

Robinson (1913b) described forma *album* to include those plants with white corollas. Corolla color ranges from purples to pale lavenders and to white in what might be termed a color continuum. To select one of these shades and give

it taxonomic rank is quite meaningless. Problems also arise due to fading of corollas on herbarium sheets. Thus names alluding to corolla color are placed in synonymy.

Wooton and Standley (1913) described *Coelestina sclerophylla* from Sonora, considering it distinct from *A. corymbosum* f. *corymbosum* because of leaf shape, pubescence, inflorescences, and a northern location. The holotype, *Merton 2031*, is beyond question *A. corymbosum* f. *corymbosum*. As there are no discontinuities in any of the above listed characters between Wooton and Standley's proposed species and *A. corymbosum* f. *corymbosum*, the name is placed in synonymy.

The chromosome number $n = 10$ is reported (Turner, Powell & King, 1962), vouchers *King 2923* and *King 3544*. An apparently unpublished record listed on *King & Soderstrom 4901* is $n = 11$. A tetraploid race, $2n = 40$, is recorded for a Michoacán collection, voucher *King 3644* (Turner, Ellison & King, 1961).

A triploid metaphase configuration varying from 10 groups of trivalents to 10 groups of univalents and 10 bivalents was seen in a preparation made from buds collected by G. B. Ownbey and J. Muggli in Michoacán. The voucher, *Ownbey & Muggli 3948* (MIN), is *A. corymbosum* f. *corymbosum* and gives no indication it might be triploid. A triploid plant would be expected to produce a high percentage of sterile pollen grains and a low percentage of viable ones. Staining the pollen with cotton blue, however, showed 95–100% good staining grains, indicating that the pollen was viable and probably not of triploid parentage. Seeds from these plants (*Ownbey & Muggli 3948*) germinated easily and quickly, also suggesting that no genetic imbalance was present. No chromosome counts from somatic cells of these plants were made, however. Measurements of the gross morphology also does not give an indication that this particular plant is triploid. It seems, then, that the buds collected in the immediate vicinity of the voucher and used for the chromosome counts came from a triploid plant, but that the voucher is from different plants which are diploid. A mixed population of diploid and tetraploid plants at this locality is suspected.

Ageratum corymbosum f. *corymbosum*, a common form of the most common species of *Ageratum* in Mexico, is distinguished by the combination of shrubby habit, heads borne in congested clusters, short petioled, ovate to ovate-lanceolate leaves with sparingly pilose upper surfaces and scabrous lower surfaces.

This forma occurs throughout Mexico with the possible exception of the Yucatan Peninsula. It extends into western Guatemala often in association with *Quercus* and *Pinus* and along roadsides and in grazed land from near sea level to ca. 2800 m elevation (Fig. 6). This form is reported from Texas (Gould, 1962), New Mexico and Arizona (Wooton & Standley, 1913; Tidestrom & Kittell, 1941), though I have not seen specimens collected in the United States. Flowers and fruits are present from July through December.

GUATEMALA. 13 miles S of Huehuetenango, *King 3389* (DS, MICH, NY, TEX, UC, US); 1.6 miles E of Chiantla, cytological voucher, *Ownbey & Muggli 3971* (MIN).

MEXICO. AGUASCALIENTES: 20.4 miles W of Aguascalientes, *Johnson & Hofstetter 1964* (MIN). CHIHUAHUA: Chihuahua, *LeSueur 70* (F, GH, MO, TEX); 35 km S of Ciudad Chihuahua, *Weber & Charette 11638* (MICH, WIS). COAHUILA: San Lorenzo Canyon, 6 miles SE of Saltillo, *Palmer 387* (F, GH, MO, NY, US). DISTRITO FEDERAL: Pedregal, *Balls B5592* (BM, GH, K, UC, US); Lomas, *Lyonnet 196* (BM, GH, K, MO, NY, US). DURANGO:

20 miles W of Durango, *Johnson & Johnson* 1768 (MIN). GUANAJUATO: Sierra de Guanajuato, *Guillemin-Tarayre* 1872 (GH). GUERRERO: 25 km WSW de Camotla, *Rzedowski* 18110 (MICH). HIDALGO: El Chico, near Pachuca, *Purpus* 1565 (F, GH, UC). JALISCO: Cerro de Talcozagua, 3–2 km E of Tapalpa, *Iltis et al.* 733 (MICH, TEX, WIS); 4.5 miles E of Tizapan on S shore of Laguna de Chapala, *Johnson & Hofstetter* 1981 (MIN); Guadalajara, *Palmer* 290 (MICH, MO, NY, US). MEXICO: La Junta, Santo Tomas, *Matuda* 29363 (NY, US). MICHOACAN: E of Zapota, *Arsène* 2678 (BM, GH, K, MO, NY, US); 21 miles E of Jiquilpan, cytological voucher, *King* 3644 (DS, MICH, NY, TEX, UC, US); ca. 22 km S of Uruapan, cytological voucher, *King & Soderstrom* 4901 (MICH, TEX, UC, US); 3.6 miles E of Morelia, cytological voucher, *Ownbey & Muggli* 3948 (MIN). MORELOS: Hillsides above Cuernavaca, *Pringle* 6234 (BM, F, GH, MICH, MIN, MSC, MO, NY, P, UC, US). NAYARIT: On road to San Blas, 1.6 miles from junction with Mexico 15, *Johnson & Hofstetter* 1977 (MIN). OAXACA: 15 miles NE of Huajuapán de León, cytological voucher, *King* 3544 (MICH, TEX). PUEBLA: Cerro Chiquihuite, near Totomihuacan, *Arsène* 2171 (GH, MO, US); 4 miles W of Izucar de Matamoros, cytological voucher, *King* 2923 (TEX). QUERETARO: 2 miles E of Querétaro, *Johnson & Ownbey* 1934 (MIN). SAN LUIS POTOSÍ: 33 km E of San Luis Potosí, *Roe et al.* 114 (MIN). SINALOA: Culiacan, *Brandeggee* s.n. (GH). SONORA: Guadalupe Canyon, *Merton* 2031 (US); 18 miles SE of Magdalena, *Wiggins* 7149 (DS, MO, TEX, US). VERA CRUZ: 5.5 miles W of Xalapa, *Johnson & Hofstetter* 2005 (MIN).

13b. *Ageratum corymbosum* Zuccag. forma *salicifolium* (Hemsl.) M. F. Johnson, stat. et comb. nov.

Ageratum salicifolium Hemsl., Biol. Contr. Amer. Bot. 2: 83. 1881. (Holotype: MEXICO.

Nayarit: Between San Blas and Tepic, *Sinclair* s.n. (K), photographs, GH, MICH.)

Ageratum strictum Hemsl., Biol. Centr. Amer. Bot. 2: 83. 1881.

Coelestina corymbosa Benth., Bot. Sulph. 111. 1844.

Carelia salicifolia (Hemsl.) Kuntze, Rev. Gen. 1: 325. 1891.

Carelia stricta (Hemsl.) Kuntze, Rev. Gen. 1: 325. 1891.

Ageratum salicifolium Hemsl. subsp. *annectens* Blake, Contr. U. S. Natl. Herb. 22: 588.

1924. (Holotype: MEXICO. Morelos: Cuernavaca, *Pringle* 9045 (US); isotype, MICH.)

Shrubs 4.5–15 dm tall; *leaves* narrowly lanceolate, 3.3–10 cm long, 0.5–1.8(–2.4) cm wide, firm, base cuneate, apex acute, margin somewhat revolute, entire to remotely crenate-dentate, scabrous, upper surface bright and shiny green to dark green, scabrous to sparingly white pilose, lower surface paler green, sparingly white pilose to more or less abundantly so at least over the 3 rather inconspicuous primary veins and reticulate secondary venation and dotted with amber to yellow glanduliferous atoms; in characters of involucre, corollas, achenes and pappus very similar to forma *corymbosum*.

This narrow-leaved form has been unquestionably accepted as a distinct species since its description by Hemsley (1881). Robinson (1913b) suggested that it may be a variety of *Ageratum corymbosum* but retained it in the rank of species. From observation in the field, especially in the type locality, I have seen forma *salicifolium* in the immediate vicinity of forma *corymbosum*. Except for the more narrow leaves of the former, the plants appear to be identical. This conspicuous similarity is noted too from herbarium specimens. Similarities are noted also in chromosome numbers, distribution and habitat, blooming time, stem and leaf pubescence, and size and shape of corollas, pappus and achenes. After studying a number of specimens, it became very evident that narrow leaves alone are not an acceptable means of distinguishing this species; variation in leaf dimensions in this species is continuous with forma *salicifolium* at the narrow extreme and forma *albiflorum* at the opposite extreme (Fig. 4). As there is no readily discernable discontinuity in morphology between the narrow-leaved pop-

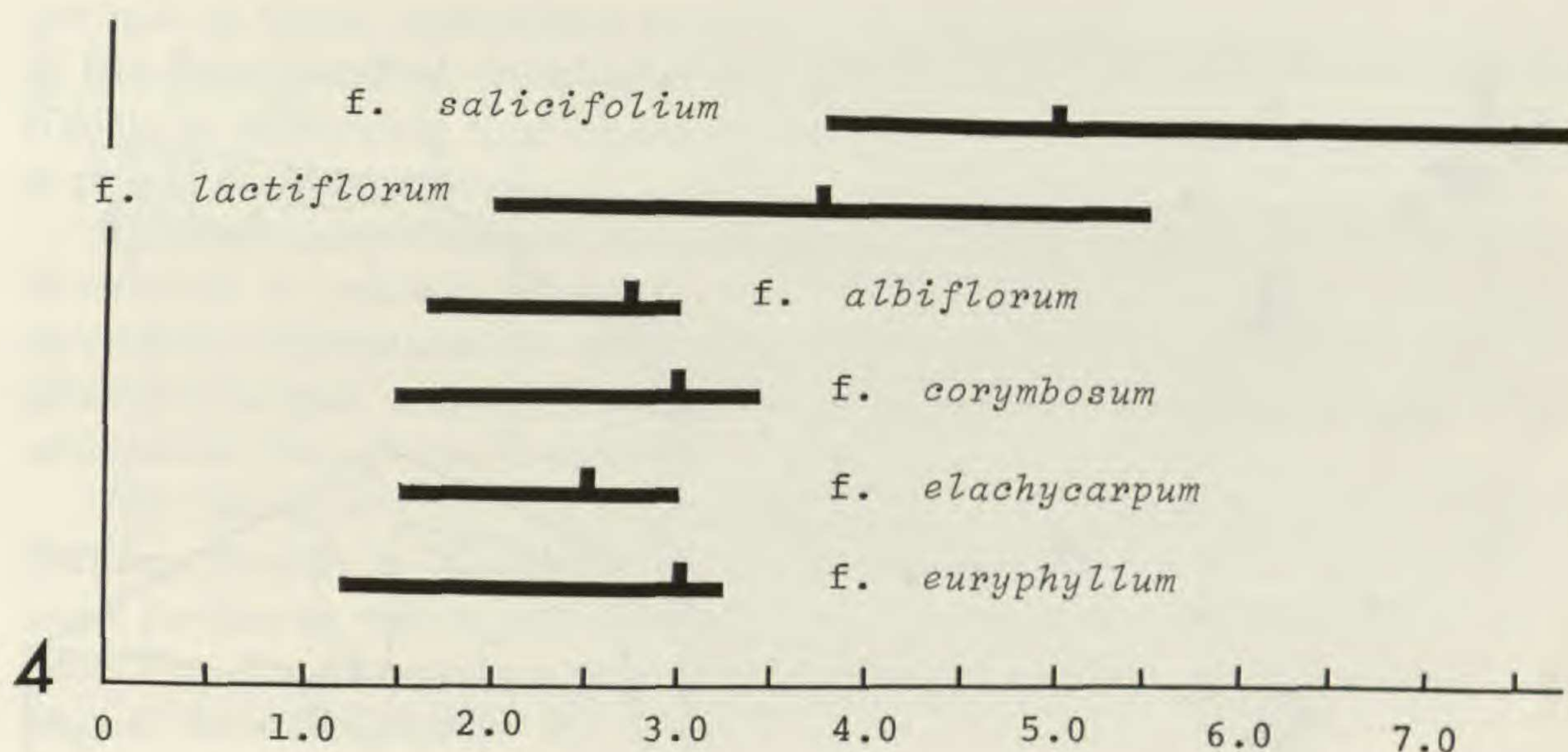


FIGURE 4. Variation in leaf length/leaf width ratio in formae of *Ageratum corymbosum* Zuccag. The median is indicated.

ulations and the remainder of the species, it is logical to consider *A. salicifolium* Hemsl. a forma of *A. corymbosum* Zuccag.

Blake (1924) saw an unusual specimen (*Pringle 9045*) on which he noted a single head bearing a very few receptacle paleae around the outer margin and from this described a new subspecies, implying that this plant provided a link between paleaceous and non-paleaceous species of section *Coelestina*. It is my opinion that Blake placed excessive importance upon the paleaceous nature of the receptacle which is present rarely and sporadically among other formae of this species as well.

Blake (1924) stated that the plant bearing the same collection number at the Gray Herbarium lacks any visible traces of receptacle paleae. I have observed this to be true on the same number at Michigan. Thus it is obvious that paleae

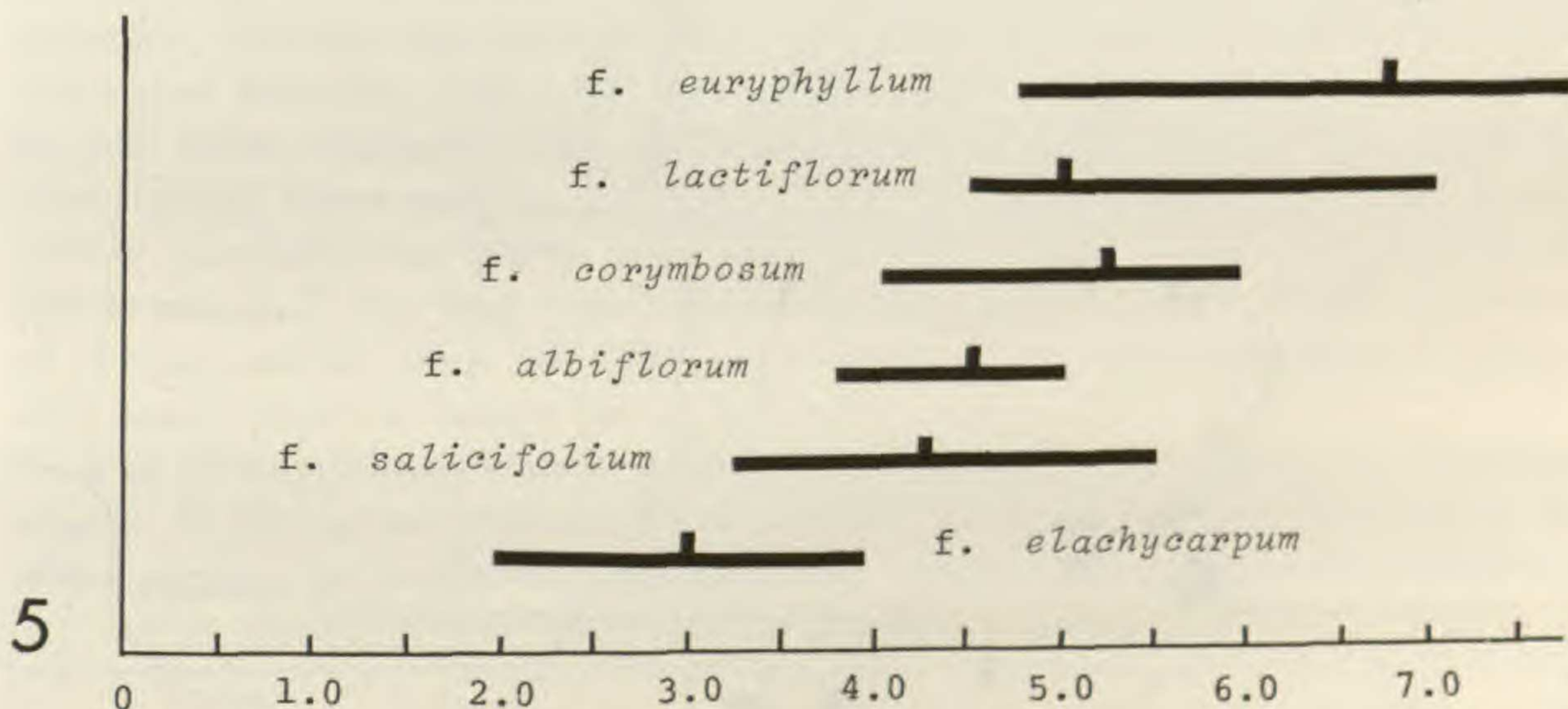
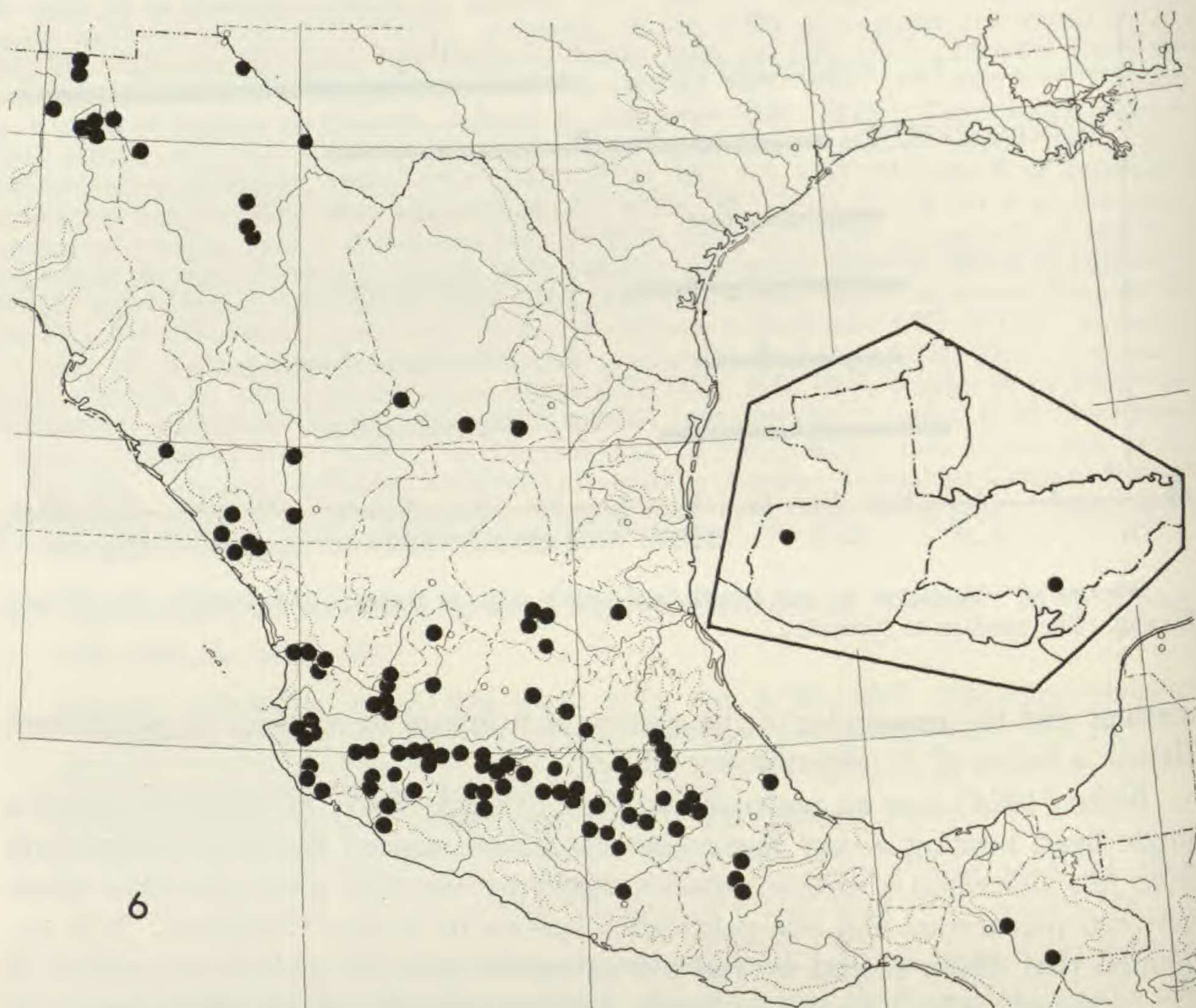


FIGURE 5. Variation in length of involucre bracts in formae of *Ageratum corymbosum* Zuccag. Length is expressed in mm, and the median is indicated.



are rare in forma *salicifolium* as paleae are not present in any other specimen of this forma studied. It is quite unnecessary to describe such abnormalities as formae or subspecies; thus *Ageratum salicifolium* Hemsl. subsp. *annectens* Blake is placed in synonymy.

Ageratum corymbosum f. *salicifolium* most closely resembles *A. corymbosum* f. *lactiflorum* in general leaf shape and in the bright green upper leaf surface sometimes encountered in the former. However, the long, narrow leaves, the subentire margins, and the inconspicuous lower surface venation distinguish forma *salicifolium* from forma *lactiflorum* and all other taxa as well.

This forma is quite common in northwest and west-central Mexico from southern Sonora to Michoacán in association with *Pinus* and *Quercus* and in moist ravines as well as dryer habitats and pastures from ca. 300–2000 m elevation (Fig. 7). Flowers are present from August through November; fruits from August through January.

MEXICO. DURANGO: ca. 6 miles N of Durango, cytological voucher, King 3750 (DS, MICH, NY, TEX, UC, US). JALISCO: Sierra de San Estebán, Barnes & Land 198 (F, K, US); *sine loc.*, Ferris 5860 (A, DS, F, US); Sierra de la Campana, along road to Mascota, McVaugh 13686 (K, MICH, US); Guadalajara, Palmer 290 (BM, GH, MICH, MO, NY, US); 6 miles W of Guadalajara, Powell & Edmondson 866 (F, MICH, TEX). MEXICO: Vigas, Temascaltepec, Hinton 1815 (BM, F, GH, MO, NY, US). MICHOACÁN: ca. 13 miles S of Uruapan, Cronquist 9749 (MICH, MSC, NY). MORELOS: Cuernavaca, Pringle 9045 (GH, MICH, US). NAYARIT: 12 miles SE of Acaponeta, Cronquist 9593 (MICH, MO, NY, TEX, US); Cerro de San Juan, SW of Tepic, Pennell 19991 (NY, US). SINALOA: 4 leagues N of La Noria, Mexia 386 (MO, UC). SONORA: Puerot de los Aserradores, White 3222 (MICH).

13c. *Ageratum corymbosum* Zuccag. forma *lactiflorum* (Robins.) M. F. Johnson, comb. nov.

Ageratum corymbosum Zuccag. var. *jaliscense* Robins. forma *lactiflorum* Robins., Contr. Gray Herb. 42: 476. 1913. (Holotype: MEXICO. Jalisco: Tequila, Palmer 351 (GH); isotypes, BM, MO, NY, US; photograph, MIN.)

Ageratum corymbosum Zuccag. var. *jaliscense* Robins., Contr. Gray Herb. 42: 476. 1913. (Holotype: MEXICO. Jalisco: Río Blanco, Palmer 715 (GH, not seen); isotype, US.)

Shrubs 5–10 dm tall; stems rarely rhizomatous; leaves elliptic-lanceolate, 4.2–8.5 cm long, 1.5–3.3 cm wide, base cuneate, entire, apex acute, margin revolute, scabrous, coarsely and conspicuously crenate-dentate, teeth at times becoming large and lobe-like, especially toward base, upper surface bright, shiny green to dull green, sparingly scabrous to pilose, venation reticulate, white, generally conspicuous, lower surface dull, pale green, short white pilose and dotted with yellow glanduliferous atoms, reticulate venation white, conspicuous; involucre bracts (4.5–)5–7 mm long, outer ones 0.65–0.8 mm wide, white pilose; characters of achene, corolla, stem coloration, and tomentum as in f. *corymbosum*, pappus also nearly identical except for an occasional seta.

The distinguishing feature of forma *lactiflorum* is the leaves as described above. At the narrow extreme, they resemble leaves of f. *salicifolium* and at the wider extreme are similar to f. *euryphyllum*. *Ageratum corymbosum* f. *lactiflorum*

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FIGURES 6–7. The distribution of *Ageratum corymbosum* in Mexico and Central America. — 6. Forma *corymbosum*. — 7. forma *salicifolium*. (Base maps copyright University of Chicago.)

is separated from f. *euryphyllum*, however, by the brighter green, narrow elliptic-lanceolate leaves with conspicuous reticulate venation and short pilose lower surfaces.

Ageratum corymbosum f. *lactiflorum* occurs in west central Mexico in rocky soil and often in association with *Quercus* from ca. 500–2500 m elevation (Fig. 8). Flowers and fruits are present from July through November.

MEXICO. AGUASCALIENTES: Near city of Aguascalientes, *Rose & Painter* 7749 (GH, NY, US). CHIHUAHUA: Rocky hills near Chihuahua, *Pringle* 669 (BM, F, GH, MICH, NY, P, UC, US). DURANGO: Tejamen, *Palmer* 486 (F, GH, MO, UC); Río Blanco, *Palmer* 715 (US); La Purísima, *Shreve* 9188 (GH, MICH, UC). JALISCO: Hacienda San Marcos, E of Volcano Colima, *Goldsmith* 81 (F, GH, MO, UC, US); Tequila, *Palmer* 351 (BM, GH, MO, NY, US). MICHOACAN: Vicinity of Morelia, W of Zapota, *Arsène* 2695 (BM, GH, K, MO, NY). SAN LUIS POTOSI: *Sine loc.*, *Parry & Palmer* 317 (F, GH, NY, P, US).

13d. *Ageratum corymbosum* Zuccag. f. *albiflorum* (Robins.) M. F. Johnson, comb. nov.

Ageratum corymbosum Zuccag. var. *latifolium* (DC.) Robins. forma *albiflorum* Robins., Contr. Gray Herb. 42: 476. 1913. (Holotype: MEXICO. Morelos: Hills near Yautepec, *Pringle* 9842 (GH); isotypes, F, NY, MO, US; photograph, MIN.)

Coelestina ageratoides HBK, Nov. Gen. Sp. Pl. 4: 151. 1820.

Coelestina ageratoides HBK var. *latifolia* DC., Prod. 5: 108. 1836.

Ageratum corymbosum Zuccag. var. *longipetiolatum* Robins., Contr. Gray Herb. 42: 477. 1913. (Holotype: MEXICO. Chihuahua: Southwestern Chihuahua, *Palmer* 110 (GH); isotypes, K, MICH, NY, US.)

Ageratum corymbosum Zuccag. var. *latifolium* (DC.) Robins., Contr. Gray Herb. 42: 476. 1913. (Holotype: MEXICO. Without collector and location (DC-G, not seen); photograph, MIN.)

Shrubs 5–15 dm tall; stems densely white pilose to subglabrous; leaves ovate to triangular-lanceolate, 4.5–8(–11.3) cm long, 2.3–4.5(–5.9) cm wide, somewhat thickened, base truncate to obtuse, apex acute to broadly so, margin crenate to dentate to subentire, slightly scabrous-pilose to pilose, rarely glandular-atomiferous, lower surface dull, pale green, densely white pilose and dotted with yellow to amber glanduliferous atoms, the 3–5 principal veins and secondary venation white, densely pilose and glandular dotted; petioles 0.5–2.6 cm long, pilose-scabrous, adaxially channeled; characters of inflorescence, involucre, corollas, achenes, and pappus as in f. *corymbosum*.

Robinson (1913b) separated his var. *longipetiolatum* and var. *latifolium* f. *albiflorum* using lanceolate-triangular leaves borne on petioles 3 cm or more long in *longipetiolatum* versus ovate leaves on shorter petioles in *latifolium* forma *albiflorum*. After studying a number of specimens, it became evident that these varieties merged readily as both leaf shape and petiole length are quite variable. The consistent and characteristic feature is the softly pubescent under surface of the leaves which was shared by both varieties as Robinson interpreted them. Distinctions between these varieties break down and the name forma *albiflorum* is applied.

Ageratum corymbosum f. *albiflorum* is distinguished among the formae by the presence of ovate to triangular-lanceolate leaves with dense pubescence on the under side which gives them a soft, downy feeling. There is a tendency toward larger leaves than in other formae, though this is by no means as con-



FIGURES 8-9. The distribution of *Ageratum corymbosum* in Mexico and Central America. — Triangle, forma *lactiflorum*; solid circle, forma *euryphyllum*. — 9. Forma *albiflorum*. (Base maps copyright University of Chicago.)

sistent as the pubescent lower leaf surfaces. *Ageratum corymbosum* f. *euryphyllum* also possesses leaves which are pubescent beneath but which are widely ovate with coarsely crenate margins.

This forma is, at times, confused with *Ageratum rugosum*, especially in Central America. However, these taxa are readily distinguished by the dark green to brown leaves in *A. rugosum* as opposed to the light green leaves in *A. corymbosum* f. *albiflorum*.

The chromosome number $n = 10$ is reported in the literature (Turner, Powell & King, 1962; Powell & Turner, 1963) and verified in this study.

This forma is widespread in Mexico, Guatemala, Honduras, and El Salvador in association with *Quercus* and *Pinus* as well as along dry roadsides and in moist ditches from ca. 100–2500 m elevation (Fig. 9). Flowers are present from June through November; fruits from July through November.

EL SALVADOR. Vicinity of Ahuachapan, *Standley & Padilla* 2908 (F).

GUATEMALA. Chinautla, *Holway* 482 (GH); SE of Huehuetenango, *Steiermark* 48173 (F).

HONDURAS. Region of El Jicarito, *Standley* 27458 (BM, F, GH, US).

MEXICO. CHIAPAS: Ca. 23 miles SE of Comitán, cytological voucher, *King* 3045 (TEX). CHIHUAHUA: 25 miles S of Batopilas, Hacienda San José, *Palmer* 31 (BM, GH, K, MICH, MO, NY, US); 1 mile from Batopilas, Hacienda San Miguel, *Palmer* 110 (GH, K, NY). DISTRITO FEDERAL: Pedregal, Tlalpam, *Seler* 4124 (GH). DURANGO: 1.8 miles W of Revolcaderos, cytological voucher, *Ownbey & Muggli* 2927 (MIN). GUANAJUATO: *Sine loc.*, *Duges* 427 (GH). GUERRERO: 28 km W of Chilpancingo, *Sharp* 441503 (NY). HIDALGO: Ixmiquilpan, *Purpus s.n.* (UC). JALISCO: Huejotitan, *Diguet s.n.* (MICH, P); 45 miles W of Sahuayo, near W end of Lake Chapala, *Powell & Edmondson* 841 (F, MICH, TEX). MEXICO: Temascaltepec, *Hinton* 2066 (BM, F, MICH, MO, NY, US). MICHOACAN: Vicinity of Morelia, *Arsène* 3227 (GH, MO, US); Apatzingan, *Hinton* 15171 (K, MICH, NY, P, UC, US). MORELOS: Hills near Yautepec, *Pringle* 9842 (F, GH, NY); mountain canyon above Cuernavaca, *Pringle* 9843 (F, GH, MO, NY, US). NAYARIT: 4 miles N of Compostela, *McVaugh & Koelz* 587 (MICH). OAXACA: Monte Alban, *Pringle* 6267 (GH). PUEBLA: Near Río Otlati, *Weaver* 954 (GH, TEX, US). SAN LUIS POTOSI: 11.8 miles N of Ciudad Valles, *Johnson & Hofstetter* 2010 (MIN). SINALOA: Baromena, *Gentry* 6113 (DS, GH, MICH, MO, NY); Lodiago, *Palmer* 1587 (F, MICH, NY, UC, US). SONORA: Conejos, *Gentry* 1112 (F). TAMAULIPAS: La Vegonia, *Bartlett* 10126 (MICH, US). TLAXCALA: Vicinity of San Vernabe Amaxac, *Hernandes* 382 (MICH). VERA CRUZ: 5 miles SE of Xalapa, *Barkley et al.* 2564 (TEX).

13e. *Ageratum corymbosum* Zuccag. forma *euryphyllum* (Robins.) M. F. Johnson, stat. et comb. nov.

Ageratum corymbosum Zuccag. var. *euryphyllum* Robins., Contr. Gray Herb. 42: 476. 1913. (Holotype: MEXICO. San Luis Potosí: Region of San Luis Potosí, *Parry & Palmer* 315 (GH); isotypes, MO, NY, US.)

Ageratum corymbosum Zuccag. var. *subsetiferum* Robins., Contr. Gray Herb. 42: 477. 1913. (Holotype: MEXICO. Zacatecas: Concepción del Oro, *Palmer* 382 (GH); isotypes, NY, US; photograph, MIN.)

Shrubs 5–10 dm tall; *leaves* widely ovate, (3–)4.2–7 cm long, (1.5–)3–4.5 cm wide, base obtuse to truncate, apex broadly acute, margin slightly revolute, scabrous, coarsely crenate to less commonly dentate, teeth large, upper surface dull, dark green, rarely bright and shiny green, finely pilose to scabrous, lower surface paler green, rather densely white pilose and dotted with yellow glandular atoms, the 3–5 primary veins and reticulate secondary venation in general not conspicuous; *involucral bracts* narrowly lanceolate, (3.5–)5–7 cm long, 0.55–

0.9(–0.15) mm wide, white pilose and at times glandular-atomiferous; *achenes* 2.25–3.25 mm long, dark black; *pappus* 0.3–0.75 mm long, margin shallowly fimbriate, at times with 1 or more setae, then the pappus 1–3 mm long; *corollas* (2.5–)2.75–3.85 mm long, in general glandular dotted and pilose.

Ageratum corymbosum f. *euryphyllum* approaches f. *lactiflorum* but is separated primarily on the basis of leaf length and width; the leaves of f. *euryphyllum* are about twice as long as wide, while those of f. *lactiflorum* are 2–5 times longer than wide. The less conspicuous leaf venation and duller green upper leaf surfaces of f. *euryphyllum* also aid in distinguishing these formae. Forma *euryphyllum* is distinct from f. *albiflorum* on the basis of wider leaves with coarsely crenate margins in the former.

Robinson (1913b) described var. *subsetiferum* employing pappus setae and elongated involucre bracts as distinguishing characters. That these characters are not consistently present in combination is immediately evident upon study of specimens. Both taxa (*euryphyllum* and *subsetiferum*) did possess widely ovate leaves with pilose lower surfaces as well as elongate involucre bracts. Pappus setae do not distinguish var. *subsetiferum*, because setae appear sporadically throughout the species. As distinctions between these varieties break down, it is desirable to consider them as one taxon under the more descriptive name, *A. corymbosum* f. *euryphyllum*.

Turner, Beaman & Rock (1961) reported the chromosome number $n = 20$ for Rock 456, a specimen with the characters of forma *euryphyllum*. Plastic peels of the lower leaf epidermis from this plant show stomatal guard cells (27–)32–38 μ long. A random sample of the leaf lower epidermis from specimens determined to be forma *euryphyllum* were measured from plastic peels. Though these plants were very similar to the tetraploid in gross morphology, the guard cells were only 15–20 μ long, suggesting that this sample is diploid throughout. Pollen from the tetraploid is 30–32 μ in diameter while pollen from a random sample is 27–34(–36) μ in diameter. As the diameter of pollen from the tetraploid is within the range of pollen size from assumed diploids, this character cannot be used as a means of determining, with certainty, diploid or polyploid populations. The evidence at hand suggests that the polyploid is rare in the population and that it can only questionably be detected by morphology, e.g., long guard cells in the tetraploid plant. It seems best to consider this forma as basically diploid with a very few widely scattered tetraploid individuals, which may be termed cryptic polyploids as they are morphologically very similar to the diploid population.

This forma occurs in northeast, northwest, and central Mexico in association with *Quercus*, on dry rocky slopes and along roadsides from ca. 500–2600 m elevation (Fig. 8). Flowers and fruits are present from June through November.

MEXICO. AGUASCALIENTES: Mountains, Hartweg 142 (BM). COAHUILA: 13 miles S of Arteago, Kenoyer & Crum 2755 (A, MICH); Saltillo, Palmer 307 (BM, F, GH, MO, MSC, NY, UC, US). DISTRITO FEDERAL: Entre Guajimalpa y Río Hondo, Matuda 26177 (NY). GUANAJUATO: Vicinity of Guanajuato, Kenoyer 1771 (A). HIDALGO: 7.4 miles E of Jacala, Johnson & Hofstetter 2007 (MIN). JALISCO: Rancho Viejo, Rzedowski 17574 (MICH). MORELOS: 20 km NE of Cuautla, Fischer 44 (MICH). NUEVO LEON: Galeana, Tayler 122 (DS, F, MO, NY, TEX, UC). PUEBLO: Acatzinco, Arsène 3604 (US). QUERETARO: Near San Juan del Río, Rose et al. 9631 (BM, GH, NY). SAN LUIS POTOSI: Alvarez, Palmer 101

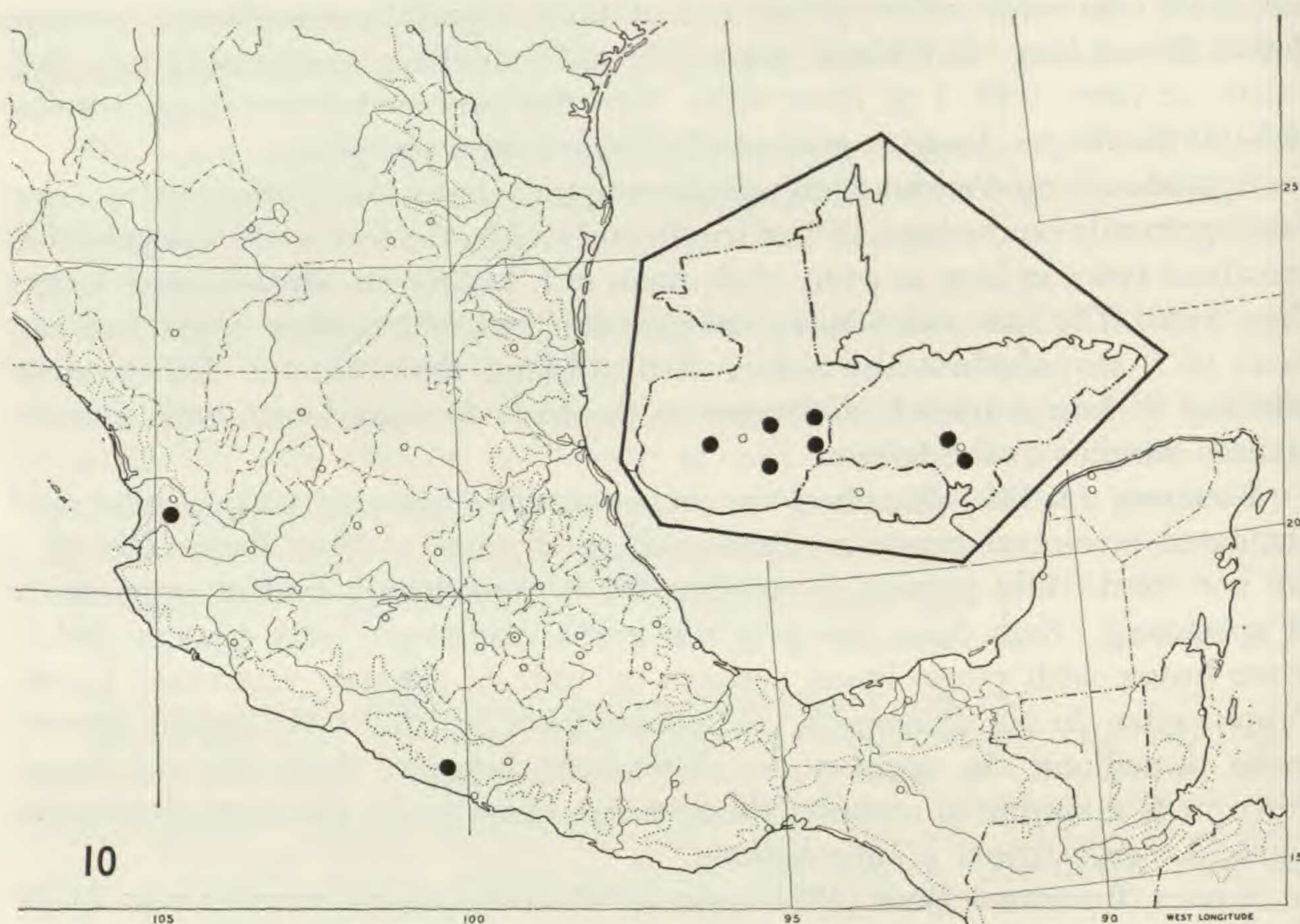


FIGURE 10. The distribution of *Ageratum corymbosum* forma *elachycarpum* in Mexico and Central America. (Base map copyright University of Chicago.)

(BM, F, GH, MSC, MO, NY, UC, US); region of San Luis Potosí, *Parry & Palmer 315* (GH, MO, NY, US), *Parry & Palmer 318* (BM, F, GH, MO, NY, US); La Capilla, cytological voucher, *Rock M-456* (TEX). TAMAULIPAS: 3 km W of Miquihauna, *Stanford et al. 643* (DS, GH, MO, NY). ZACATECAS: S slope of La Bufa, Zacatecas, *Dressler 186* (GH, MO); Concepción del Oro, *Palmer 382* (GH, NY, US).

13f. *Ageratum corymbosum* Zuccag. forma *elachycarpum* (Robins.) M. F. Johnson, stat. et comb. nov.

Ageratum elachycarpum Robins., Contr. Gray Herb. 42: 477. 1913. (Holotype: GUATEMALA. Dept. Santa Rosa: Santa Rosa, *Heyde & Lux 4228* (GH, not seen); isotypes, F, K, US.)

Shrubs to 20 dm tall; leaves ovate to lanceolate, ca. 5–8(–11) cm long, 2.2–5.5 cm wide, thin to more or less firm, base obtuse to truncate, apex acute margin crenate to dentate, somewhat revolute, scabrous, upper surface dull, dark green, scabrous, lower surface pale green, white pilose, at times densely so, conspicuously dotted with yellow to amber glandular atoms to subglabrous, the 3 primary veins prominent, secondary venation reticulate; petioles 0.5–2.5(–5) cm long, pilose-puberulous to scabrous; involucral bracts lanceolate, (2.05–)2.4–3.5(–4) mm high, an outer one 0.55–0.65(–0.95) mm wide, pale green, white pilose at times with glandular atoms, prominently 2-ribbed basally, margin entire, herbaceous to scarious, apex acute; corollas narrowly funnelform, (1.75–)2–2.35 mm long, tube and throat white, short white pilose and sparingly dotted with yellow glandular atoms, lobes blue to lavender, acute, sparingly pilose to glabrous; achenes 1.2–

1.65(–1.75) mm long, black; *pappus* 0.25–0.35 mm long, margin entire to shallowly lobed.

The characters listed in the above key, namely, achenes and involucre bracts shorter than those found in the remainder of the species, prompted Robinson (1913b) to describe this taxon as a species separate from *A. corymbosum*. It is my opinion, however, that the overall features of the plant as well as similar habitat, tomentum, and size and shape of *pappus* and corollas indicate a very close relationship to *A. corymbosum*. The short bracts and achenes are merely one end of a continuum which leads from this extreme to the opposite found in forma *euryphyllum* and forma *lactiflorum* (Fig. 5). As no real discontinuity exists between forma *elachycarpum* and the other formae of this species, it is my opinion that these plants with shorter achenes and bracts should be considered a forma, not a separate species.

In general, this forma grows to the south of the other formae and in the area where the similar *A. rugosum* occurs. Though these taxa may be confused by collectors, the short achenes, involucre bracts, and leaves as well as less dense pubescence on the lower leaf surfaces and involucre bracts set f. *elachycarpum* apart from *A. rugosum*.

Ageratum corymbosum f. *elachycarpum* occurs in Guatemala and Honduras with a disjunction to Guerrero and Nayarit in Mexico, in association with *Quercus* from ca. 500–1000 m elevation (Fig. 10). Flowers are present from July through January; fruits from August to January.

GUATEMALA. Santa Rosa, Heyde & Lux 4228 (F, K, US); near Jalapa, Kellerman 7969 (NY); Barranca del Incarnación, Skinner s.n. (K); between Chimaltenango and San Martín Jilotepeque, Standley 64432 (F, GH); lower slopes of Sierra de las Minas, Steyermark 29529 (F, GH); vicinity of Montana Cebollas, Steyermark 31296 (F).

HONDURAS. Cerro de Hule, 20 km S of Tegucigalpa, Molina 18462 (F); between Los Laureles and Las Tapias, NW of Tegucigalpa, Molina 18577 (F).

MEXICO. GUERRERO: Montes de Oca, Hinton 10596 (GH, NY, US); Vallecito, Langlasse 310 (GH, K, US). NAYARIT: 9 miles N of Compostela, McVaugh & Koelz 526 (MICH).

14. *Ageratum rugosum* Coult., Bot. Gaz. 20: 42. 1895.

Holotype: GUATEMALA. Dept. Santa Rosa: Santa Rosa, Heyde & Lux 4243 (US); photograph, F; tracing and small fragment, GH.

Shrubby *perennial* to 24 dm tall; *roots* fibrous, arising adventitiously from perennial stem base; *stem* erect, branched, reddish when young, to gray, white to tawny puberulous-tomentose throughout, most conspicuously on younger parts, also with scattered amber colored atomiferous glands; *leaves* opposite, rarely alternate above, petioled, ovate, 4–8.5(–12) cm long, 2.4–4.5(–6.5) cm wide, base obtuse to rarely truncate, apex acute, margin crenate to very obscurely so, upper surface conspicuously dark green to brownish, smooth or less commonly rugulose, pilose to scabrous throughout, puberulous over the 3 conspicuous veins, lower surface paler green, abundantly white tomentose at least over the 3 prominent primary veins and secondary reticulate veins, with amber or yellow atomiferous glands or eglandular; *petioles* ca. 0.3–2.5(–3) cm long, abundantly puberulent and tomentose; *inflorescences* terminal, the 3 to ca. 20 heads grouped in corymbose clusters; *peduncles* coarse, bracteolate, densely brown to white puberulent and

TABLE 4. A comparison of *Ageratum rugosum* and *A. tomentosum* sens. lat.

Character	<i>A. rugosum</i>	<i>A. tomentosum</i> s.l.
Habit.	Shrubs to 24 dm tall with fibrous roots.	Shrubs to 5 dm tall with woody taproots.
Leaves.	Ovate, 4–8.5(–12) cm long, 2.4–4.5(–6.5) cm wide, upper surface dark green, tomentum beneath dense, variable.	Deltoid to ovate, (1.6–)2–3.5(–4.1) cm long, 1.1–2.7(–3) cm wide, bright green above, tomentum beneath always dense.
Distribution.	Central America, very southern Mexico, Vera Cruz.	East central and southern Mexico.

tomentose, with glandular atoms; *bracteoles* alternate, puberulent and tomentose, *ca.* 0.5 cm long; *involucres* hemispheric, spreading when older, bracts biseriate, firm lanceolate, 2-ribbed, (3.8–)4–5(–5.5) mm long, outer ones (0.5–)0.6–0.95 mm wide, greenish throughout or apically reddish-purple, densely white pilose or the hairs scattered, also with scattered yellow glandular atoms or eglandular, margin entire, apex acute, inner bracts lanceolate to spatulate, less densely pilose; *corollas* tubular to narrowly funnelform, 2.25–2.6(–3.15) mm long, pilose and glandular atomiferous to nearly glabrous, tube pale green to white, throat pale green to lavender, pale violet or light blue, rarely white; *achenes* 5-angled, dark brown to black, 1.5–2(–2.15) mm long, glabrous, tapering toward small carpodium; *pappus* coroniform, tawny, 0.25–0.5 mm high, margin entire to irregularly dentate, less commonly with 1–5 firm setae, then pappus 1.25–1.5 mm long.

Coulter (1895) placed *Ageratum rugosum* near *A. conyzoides* because of the presence of awned pappus scales in both. Robinson (1913*b*) followed this concept. After studying a considerable number of specimens, it became evident to me that the awned pappus scales are of a very different nature in *A. rugosum* and *A. conyzoides*. The usual pappus of *A. rugosum* is a coroniform cup-like structure which only rarely has 1–5 subulate awns which are invariably fused into the cup-like basal ring. In *A. conyzoides*, on the other hand, the pappus setae are flat, membranous, marginally erose and basally free. This single character suggests that *A. rugosum* is probably more closely allied to the group of species with a similar pappus.

Ageratum rugosum is often identified as *A. corymbosum* or *A. tomentosum*. Though similar in growth habit and general appearance to *A. corymbosum*, *A. rugosum* is distinguished by the conspicuous dark green, ovate leaves with the densely white tomentose lower surfaces and the generally more pilose involucre bracts. *Ageratum rugosum* also occurs farther south than does the greater part of *A. corymbosum* sens. lat. *Ageratum rugosum* is distinguished from *A. tomentosum* as summarized in Table 4.

Ageratum rugosum is similar to *A. nelsonii* in leaf shape and size as well as coloration and pubescence of the leaves but is distinguished by the small heads, receptacle paleae, and the shorter pappus of the latter.

Turner, Ellison & King (1961) published the chromosome number $n = 20$ for

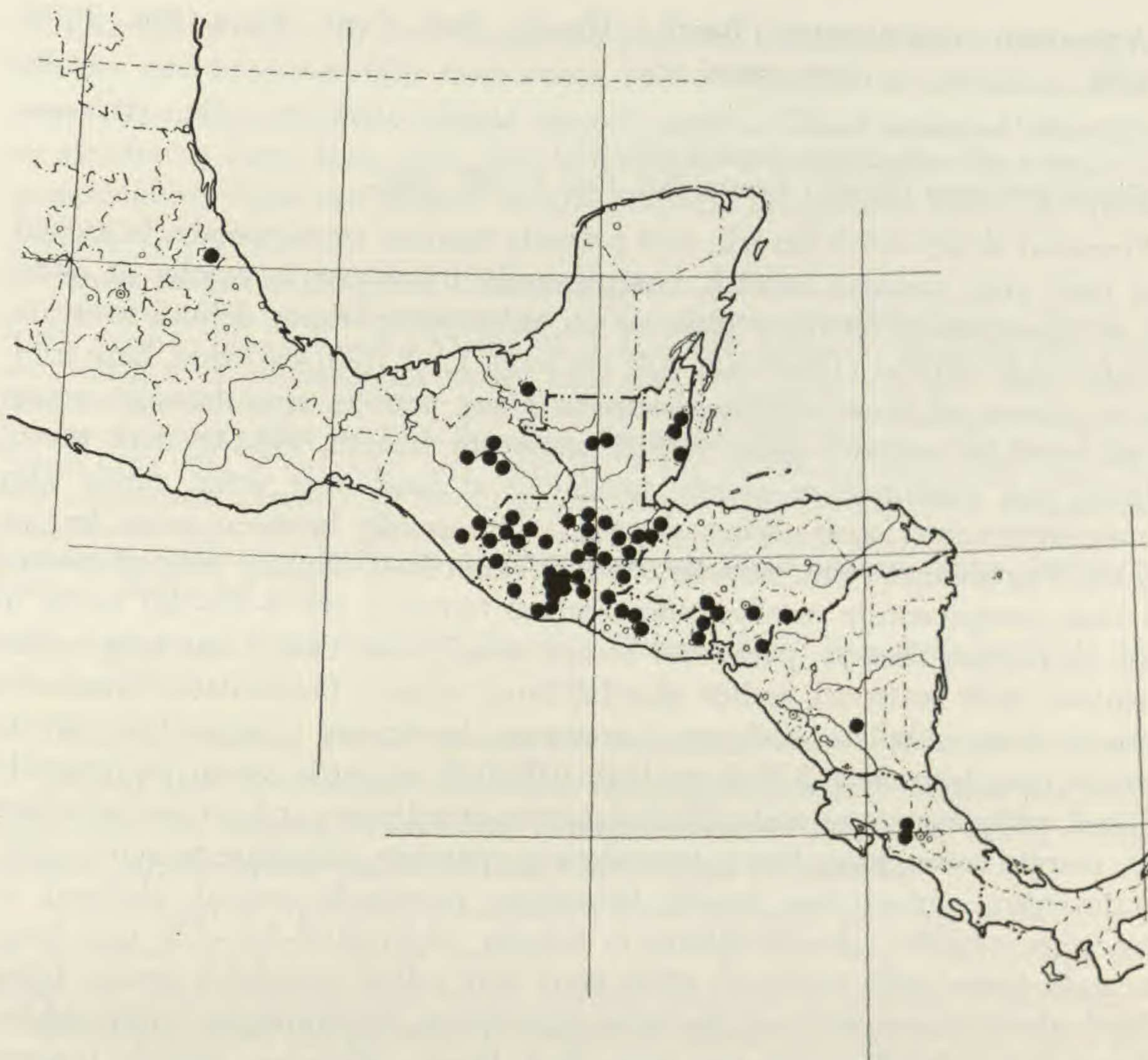


FIGURE 11. The distribution of *Ageratum rugosum* in Mexico and Central America. (Base map copyright University of Chicago.)

Ageratum corymbosum, voucher King 3291. I find this specimen to be *A. rugosum*, and the tetraploid number should refer to this taxon.

This species occurs from southern Chiapas to Panama (there is a single collection from central Vera Cruz) on rocky and/or brushy slopes, in open fields, pine and oak forests and often in moist conditions, rarely above 2800 m elevation (Fig. 11). It flowers throughout the year, but most commonly from October through May.

BRITISH HONDURAS. Pine Ridge, Butcher Burn, Bartlett 11396 (F, GH, MICH, MO, US); All Pines, Schipp 738 (A, BM, F, GH, K, MICH, MO, NY, UC).

COSTA RICA. La Palma de San Ramón, Brenes 5804 (F).

EL SALVADOR. Vicinity of San Marcos, Standley 22777 (GH, NY, US).

GUATEMALA. La Libertad, Aguilar 15 (A, GH, MICH, MO); Santa Rosa, Heyde & Lux 4243 (US); 15 miles N of Salama, cytological voucher, King 3291 (TEX); Santa Maria de Jesus, Standley 66828 (F); barrancos 6 miles S and W of Tajumulco, Steyermark 36589 (F).

HONDURAS. Río El Quebracho, above El Jicarito, Standley 14799 (F); slopes of Cerro Majicoran, Williams 16935 (F).

MEXICO. CHIAPAS: 45 km E of Ocosingo, Dressler 1633 (GH, MICH, US); Mt. Ovando, Matuda 3968 (GH, MICH, MO, NY); Zamapam, Purpus 10863 (GH, US). VERA CRUZ: Zacuapam, Purpus 14051 (A, DS, F, GH, NY).

NICARAGUA. Along road to La Cantera and Los Pinos, SW of Jinotega, Standley 10122 (F).

15. *Ageratum tomentosum* (Benth.) Hemsl., Biol. Cent. Amer. Bot. 2: 82. 1881.

Coelestina tomentosa Benth. in Oerst., Vidensk. Meddel. 1852: 71. 1852. (Holotype: COSTA RICA: Candelaria, Oersted 163 (K).)

Carelia tomentosa (Benth.) Kuntze, Rev. Gen. 1: 325. 1891.

Perennial *shrubs* 2.5–5 dm tall; *root* a woody taproot; *stems* woody, branched, older bark gray, younger reddish, conspicuously tomentose to woolly at nodes and on young shoots, at times glabrous on older parts; *leaves* deltoid to ovate, less commonly elliptic, (1.6–)2–3.5(–4.1) cm long, 1.1–2.7(–3) cm wide, base truncate to obtuse, at times slightly decurrent along petiole, apex broadly acute, margin revolute, crenate, upper surface rugose to smooth, light to dark green, scabrous and tomentose or merely tomentose at least over veins, rarely also farinose over veins, lower surface densely white woolly between veins, less so over the 3 prominent veins; *petioles* 0.6–1(–1.7) cm long, slightly winged toward leaf base, conspicuously woolly; *inflorescences* terminal, the 6–12(–22) heads in dense corymbose clusters; *peduncles* coarse, usually less than 1 cm long, white tomentose with scattered amber glanduliferous atoms, bracteolate; *bracteoles* alternate, firm, subulate, scabrous, tomentose; *involucres* campanulate, bracts biseriate, firm, lanceolate, 3.75–5 mm high, 0.65–0.85 mm wide, green, prominently 2-ribbed, white tomentose and yellow glandular-atomiferous at least toward acute apex, margin entire, inner bracts lanceolate to spatulate, attenuate to acute apex, margin entire, surface less densely tomentose; *receptacle* conical, glabrous or paleaceous; *corollas* infundibuliform to tubular, (2.25–)2.65–3.1(–3.5) mm long, tube pale green, with scattered white hairs and yellow glandular atoms, lobes deltoid, obtuse, tomentose and glandular-atomiferous, bluish-purple, rarely white; *achenes* (1.6–)1.9–2.65(–2.75) mm long, dark brown, glabrous, slightly tapered toward inconspicuous carpopodium; *pappus* coroniform, 0.3–0.55 mm high, margin slightly undulate to shallowly pectinate.

This species can be divided into two formae based upon the presence or absence of receptacle paleae.

- | | |
|--------------------------------|--|
| 1. Receptacle glabrous | 15a. <i>A. tomentosum</i> f. <i>tomentosum</i> . |
| 1. Receptacle paleaceous | 15b. <i>A. tomentosum</i> f. <i>bracteatum</i> . |

15a. *Ageratum tomentosum* (Benth.) Hemsl. forma *tomentosum*.

The type locality is questioned here because the indices to maps do not list Candelaria, Costa Rica. As the remainder of this taxon is found in Central Mexico, one wonders if the type locality may be given incorrectly on the label with the type.

Ageratum tomentosum f. *tomentosum* is often confused with *A. rugosum* but can be readily distinguished (also see discussion under *A. rugosum*). The generally short, shrubby habit, taproot, and deltoid leaves, the lower surfaces of which are densely and conspicuously white woolly, serve to distinguish this attractive taxon from all others.

The chromosome number $n = 10$ is reported (Turner, Beaman & Rock, 1961), voucher King 3548. The collection number 3458 was mistakenly given in publication.

This forma occurs in east-central and southern Mexico in dry sandy soil, rocky hillsides and limestone hills from about 1600–2000(–2500) m elevation. It is reported from Guatemala and Costa Rica (Hemsley, 1881; Standley, 1928), though no specimens have been seen from Guatemala and the Costa Rica location is questionable. Buds are present in June; flowers are present from July through August(–December).

COSTA RICA (?): Candelaria, *Oersted* 163 (K).

MEXICO: *Sine loc.*, *Schlumberger* s.n. (NY). OAXACA: Tomellin Canyon, *Pringle* 5786 (GH). PUEBLA: Road side gravel 5 miles NE of Zapotitlan, *Johnson & Hofstetter* 2002 (MIN); ca. 7 miles N of Puebla-Oaxaca border, *King* 3548 (NY, TEX, UC, US); near Tehuacan, *Rose, Painter & Rose* 10161 (GH, US); between Nacozacoalco and San Antonio Canada, *Smith, Peterson & Todega* 4084 (F, US); Esperanza, *Pittier* 434 (US); limestone hills near Tehuacan, *Pringle* 6754 (BM, F, GH, MIN, MO, MSC, NY, P, UC, US); *Pringle* 9522 (GH, MICH, MSC, MO); Esperanza, *Purpus* 1129 (P); Tehuacan, *Purpus* 1179 (F, GH, US); Barranca de las Pilas, *Purpus* s.n. (US). VERA CRUZ: Valle d'Orizaba, *Bourgeau* 2924 (F, GH, K, P); Lepinziana, *Mohr* s.n. (US); shrubby mountain top W of Orizaba, *Sharp* 44864 (NY); Maltrata, *Seaton* 346 (US).

15b. *Ageratum tomentosum* (Benth.) Hemsl. forma **bracteatum** M. F. Johnson, forma nov.

Holotype: MEXICO. Puebla: 12 miles S of Zapotitlan, *Johnson & Hofstetter* 2001 (MIN).

Differt ab *A. tomentosum* f. *tomentosum* receptaculo paleaceo. Paleae lanceolatae, 3.85–5.25 mm longae, 0.3–0.4 mm latae, 2-costatae, cacumine acuto, margine integro, superficiebus glabris vel cacumen versus tomentillis.

Very similar to *Ageratum tomentosum* f. *tomentosum*, differing in the presence of receptacle paleae. *Paleae* lanceolate, 3.85–5.25 mm long, 0.3–0.4 mm wide, 2-ribbed, apex acute, margin entire, surface glabrous or apically tomentose.

Robinson noted the presence of receptacle paleae on *Purpus* 2547 (F), as he wrote on an annotation label "forma paleis paucis instructo." But he did not recognize the paleaceous form in his revision.

The paleaceous plants are often found in close association with non-paleaceous ones, and both are assigned the same collection number when collected together. *King* 3548, the voucher for the chromosome number $n = 10$ (Turner, Beaman & Rock, 1961), is a collection of paleaceous and non-paleaceous plants. The exact plant from which the chromosome count was made is not known.

Ageratum tomentosum f. *bracteatum* occurs in Chiapas, Oaxaca, Puebla, and Vera Cruz often on limestone or sandstone and among *Pinus* and *Quercus*. Flowering dates are the same as in f. *tomentosum*.

MEXICO. CHIAPAS: Pine and oak forest, near Fenis, *Purpus* 10059 (NY). OAXACA: Valley of Oaxaca, *Nelson* 1213 (GH, US); Sierra de la Yerba, in the vicinity of San Luis Tultitlanapa, near Oaxaca, *Purpus* 2547 (BM, F, GH, MO, UC, US); scattered over steep rocky sandstone slope 12 miles S of Zapotitlan, *Johnson & Hofstetter* 2001 (MIN); 7 miles N of the Puebla-Oaxaca border, *King* 3548 (DS, MICH); limestone hills near Tehuacan, *Pringle* 9522 (US). PUEBLA: Near Tehuacan, *Rose & Hay* 5877 (US). VERA CRUZ: Maltrata, near Mt. Orizaba, *Seaton* 346 (F, GH).

16. *Ageratum standleyi* Robins. in Standley, Jour. Arnold Arbor. 11: 44. 1930.

Holotype: HONDURAS. Dept. de Comayagua: Pine forest in vicinity of Siguatepeque, *Standley* 56234 (F); isotypes, A, US.

Perennial shrubs 3–6.5(–9) dm tall; roots fibrous, coarse, woody; stem woody from a basal caudex, branched, older parts gray, glabrous, younger parts dark

TABLE 5. A comparison of *Ageratum standleyi*, *A. chortianum*, and *A. tomentosum* sens. lat.

Character	<i>A. standleyi</i>	<i>A. chortianum</i>	<i>A. tomentosum</i> s.l.
Leaves.	Ovate, glandular-punctate above, 2–3.5 cm long, margin entire.	Lanceolate, eglandular, (3.5–)5–6 cm long, margin entire to crenate.	Deltoid to ovate, eglandular, 2–3.5 cm long, margin crenate.
Petioles.	0.1–0.4 cm long.	0.7–0.8 cm long.	0.6–1.7 cm long.
Corollas.	2–2.2 mm long.	About 2 mm long.	2.25–3.5 mm long.
Involucre.	3.5–4.5 mm long.	4.75–5 mm long.	3.75–5.4 mm long.
Roots.	Fibrous.	Unknown.	Taproot.
Distribution.	Honduras.	Guatemala and Honduras.	Mexico.

red, with white scabrous-puberulent hairs, becoming mixed with amber glandular atoms toward inflorescences; *leaves* opposite, short petioled, xeromorphic, ovate, 2–3.5 cm long, 1–2 cm wide, base obtuse, entire, apex acute, margin entire, somewhat thickened, revolute, upper surface dull green, amber glandular-punctate, at times scabrous, puberulent and/or scabrous over the white veins, lower surface densely white to gray tomentose with scattered amber glandular atoms, veins prominent, 3-veined to pinnately veined; *petioles* 0.1–0.4 cm long, densely white scabrous-puberulent with scattered amber glandular atoms; *inflorescences* terminal, the 4–12 heads in a dense corymbose cluster; *peduncles* ca. 0.4–1 cm long, bracteolate, densely white scabrous-puberulent with mixed amber glandular atoms; *bracteoles* alternate, linear, to 4 mm long, puberulent with glandular atoms; *involucres* campanulate, bracts biseriate, firm, 2-ribbed, lanceolate, 3.5–4.5 mm high, 0.5–0.65 mm wide, green to deep red, puberulous and amber glandular-atomiferous at least basally, margin entire, apex acute; *corollas* funnel-form, 2–2.2 mm long, puberulous and glandular atomiferous over the greenish or white tube and throat, the 5 lobes pale lavender to bluish, or white; *achenes* 5-angled, glistening black, 1.5–2.1 mm long, glabrous, slightly tapering toward white carpodium; *pappus* coroniform, 0.15–0.25(–0.4) mm high, light brown, margin irregularly short dentate.

Ageratum standleyi is a very distinctive species and not easily confused with another, though similarities with *A. tomentosum* sens. lat. and *A. chortianum* are evident in leaf tomentum and shrubby habit. Table 5 summarizes the distinctive characters of these species.

Standley and Steyermark (1944) placed high taxonomic value upon the pinnately nerved leaves of *Ageratum chortianum* as opposed to the 3-veined leaves of *A. standleyi*. This feature, while consistent in the limited material of *A. chortianum* available, is not in *A. standleyi*, as both pinnately nerved and 3-nerved leaves are present on the same specimen. The other characters listed above are more consistent and serve well to separate these species.

This species is apparently endemic to Honduras in rocky *Pinus-Quercus*

forests from *ca.* 780–1700 m elevation (Fig. 13). Flowers and fruits are present from July through February; fruits are dispersing in January and February.

HONDURAS. COMAYAGUA: Vicinity of Siguatepeque, *Standley* 55853 (US), *Standley* 56234 (A, F, US). EL PARAISO: Vicinity of El Zamorano, *Standley* 1498 (F); Pinares Norte de Yuscaran, *Standley* 28569 (US); cumbre NW of Cuinope, *Standley et al.* 2033 (F); along Manzaragua road, near Guinope, *Williams* 15829 (BM, GH, US). MORAZAN: Uyuca, *Glassman* 2130 (MIN, NY); entre Las Mesas y Guayabillas, *Molina* 13163 (F); between Cuesta de las Muertos and Monte Oscuro near La Montanita, *Molina* 14686 (F); Chaquito, *Rodriguez* 389 (F); Zamorano, *Rodriguez* 643 (F); San Antonio de Oriente, *Rodriguez* 686 (F); slopes of Cerro de Uyuca, region of El Valle Encantando, *Standley et al.* 960 (F); El Zamorano, *Standley* 11761 (F), *Standley* 12146 (F); Cerro de La Zopiloteria, vicinity of El Zamorano, *Standley* 14545 (F), *Standley* 22025 (F); mountain slopes along Río Agua Amarilla NW of El Zamorano, *Standley* 23272 (F); Piedra Herrada, W slope of Cerro de Uyuca, *Standley* 23712 (F); above El Zamorano, *Standley* 26608 (F); near Joya Grande, on road from El Zamorano to Suyapa, *Standley & Molina* 4485 (F); rocky hillside near Las Mesas, *Williams* 17243 (F, GH); along Santa Clara Creek, *Williams & Molina* 15874 (F); near Las Mesas, *Williams, Rua & Williams* 18936 (F).

17. *Ageratum chortianum* Standl. & Steyerl., Publ. Field Mus. Nat. Hist., Bot. Ser. 23: 98. 1944.

Holotype: GUATEMALA. Dept. Chiquemala: Near Montana Cebollas, along Río Santa Lucia Saso, SE of Quezaltepeque, *Steyermark* 31269 (F).

Perennial *shrub ca.* 1.3 dm tall; *roots* unknown; *stem* woody, branched, bark gray to tan, densely white-scabrous to puberulous-scabrous above, older parts glabrous, eglandular-atomiferous throughout, leafy nearly to inflorescences; *leaves* coriaceous, opposite, petioled, lanceolate, the longest 5–6(–6.5) cm long, 1.5–2.6 cm wide, base obtuse, margin revolute, entire, apex acute to widely so, upper surface dark green, scabrous, puberulous-scabrous over midrib and prominent secondary veins, eglandular-atomiferous, lower surface densely white tomentose, eglandular, rarely with widely scattered glandular atoms, venation pinnate or 3-veined; *petioles* 0.7–0.8 cm long, very densely white to tawny puberulous-pilose; *inflorescences* terminal, the 4–5 or more heads grouped in a corymbose cluster; *peduncles ca.* 3–6 mm long, densely white to tawny pilose-puberulent, bracteolate; *bracteoles* alternate, 3–5 mm long, green, linear, pilose-puberulent; *involucres* campanulate, bracts bi- to triseriate, prominently 2-ribbed basally, dark green, lanceolate, middle and inner-most series (3.25–)4.75–5 mm long, 0.55–0.65 mm wide, outer ones about $\frac{1}{2}$ as long, short white pilose overall, margin ciliate, tapering to an acute apex; *corollas* narrowly funnelform, 2.25–2.45 mm long, externally pilose throughout, tube and narrow throat white (?), lobes lavender to white; *achenes* 5-angled, brown, 1.75–2 mm long, glabrous, slightly tapered toward inconspicuous carpopodium; *pappus* coroniform, *ca.* 0.25 mm long, tawny, margin undulate to minutely dentate.

Ageratum chortianum is known from relatively few collections all of which are incomplete, as only the upper branches are preserved.

Standley and Steyermark (1944) described this species as closely related to *Ageratum standleyi*. Though both species possess similar coriaceous or xeromorphic leaves with dense tomentum on the lower surfaces and a shrubby habit, these shared characters need not indicate relationship but rather may be the result of convergence of these species in a similar environment.

Ageratum chortianum is distinguished from other species by the lanceolate, eglandular, coriaceous leaves. Standley and Steyermark (1944) are of the opinion that the pinnate venation of *A. chortianum* versus three principal veins in *A. standleyi* is an important distinguishing feature. However, this characteristic is not consistent; both venation types are present in *A. standleyi* as well as in *A. chortianum*. Also, see the discussion under *A. standleyi* presented here.

Ageratum chortianum occurs in Honduras and Guatemala on dry hills in pine forests and from ca. 600–1000 m elevation (Fig. 13). Flowers and fruits are present from March to November.

GUATEMALA. CHIQUIMULA: Montaña Castilla, vicinity of Montaña Cebollas, along Río Lucia Saso, 3 miles SE of Quezaltepeque, Steyermark 31269 (F). GUATEMALA: Without locality, Aguilar 134 (F). JALAPA: 10 miles S of Jalapa, Steyermark 32218 (F).

HONDURAS. CORTES: Montaña La Cumbra, caserio Las Pinitas, Molina 10523 (F), Molina 10585 (F). SANTA BARBARA: Los Dragos, on Río Chamelecon, SW of Quimistan, Standley & Lindelie 7486 (F), Standley & Lindelie 7498 (F, UC).

18. *Ageratum guatemalense* sp. nov.

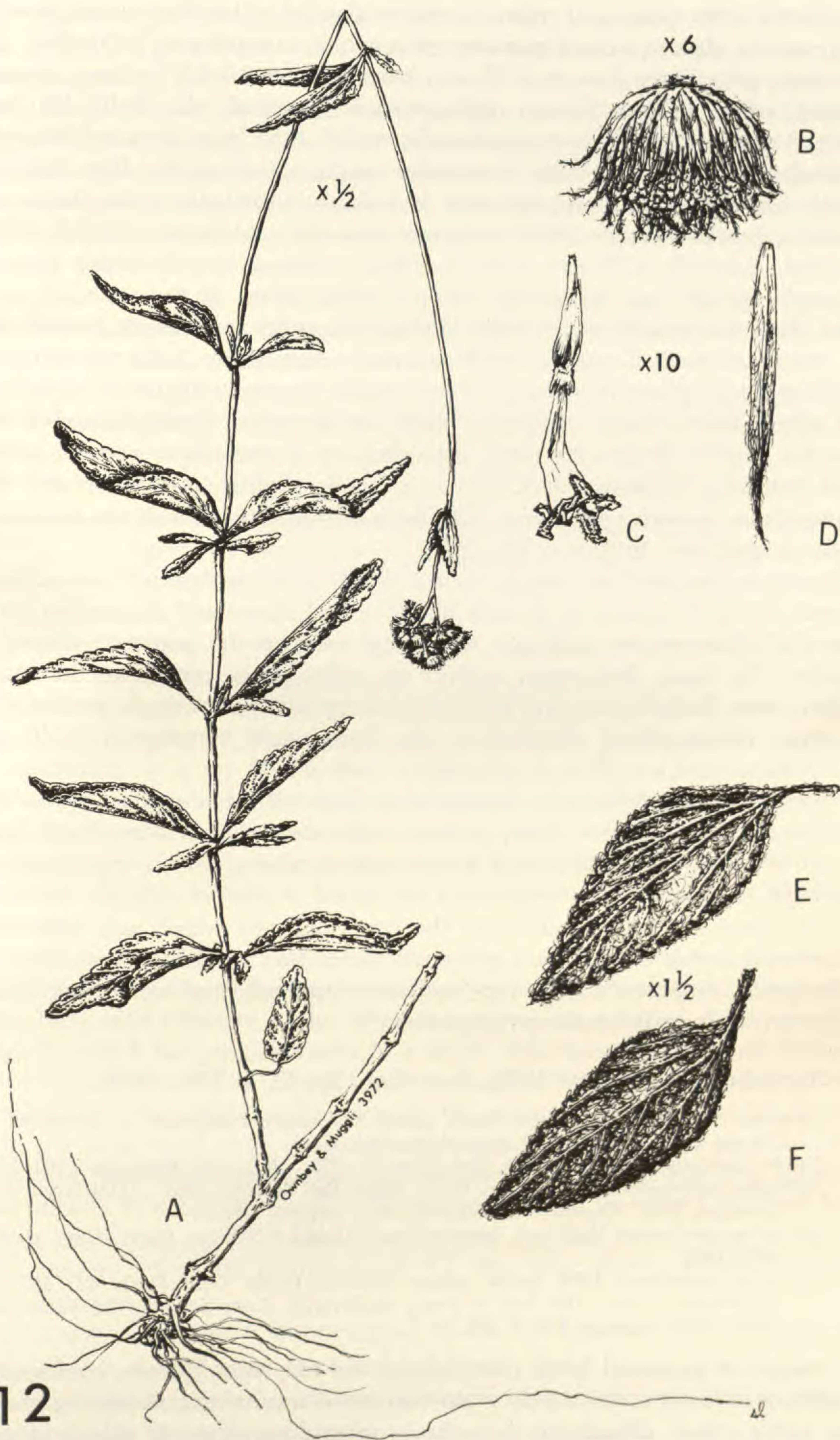
Holotype: GUATEMALA: Totonipacan ca. 22 miles S of main turnoff to Huehuetenango, Ownbey & Muggli 3972 (MIN).

Caulis erectus, simplex, plerumque ramosus ad corymbos, cortice fusco-cinereo obscure rubescente ad cacumen, incano-puberulo vel scabro-puberulo interdum valde dense sed subglabrescente ramulos supernos versus. Folia opposita, remota a corymbis, breviter petiolata, aliquantum crassa et carnosae, velutata, lanceolata vel lanceolate-elliptica, (2.7–)3.1–4.4 cm longa, 1.1–1.4 cm lata, base cuneato-attenuata, integra, margine revoluta, crenata, apicem versus gradatim integro, scabro-puberulo, nonnumquam purpureo, apice attenuato, acuto, in pagina superiore flavovirentia vel virentia, manifeste incano-pilosa, gradatim scabra ad marginem, venis non manifestis; in pagina inferiore folia flavovirentia, manifeste incano-pilosa, cum glandulo-granulosa vel flaventia vel sucinea punctulis, rarius glabra, 3 venis albis manifestis. Involucra campanulata, squamis anguste lanceolatis vel linearibus (3–)3.5–4.75(–5) mm alta, 0.4–0.65 mm lata. Receptaculum conicum, nudum.

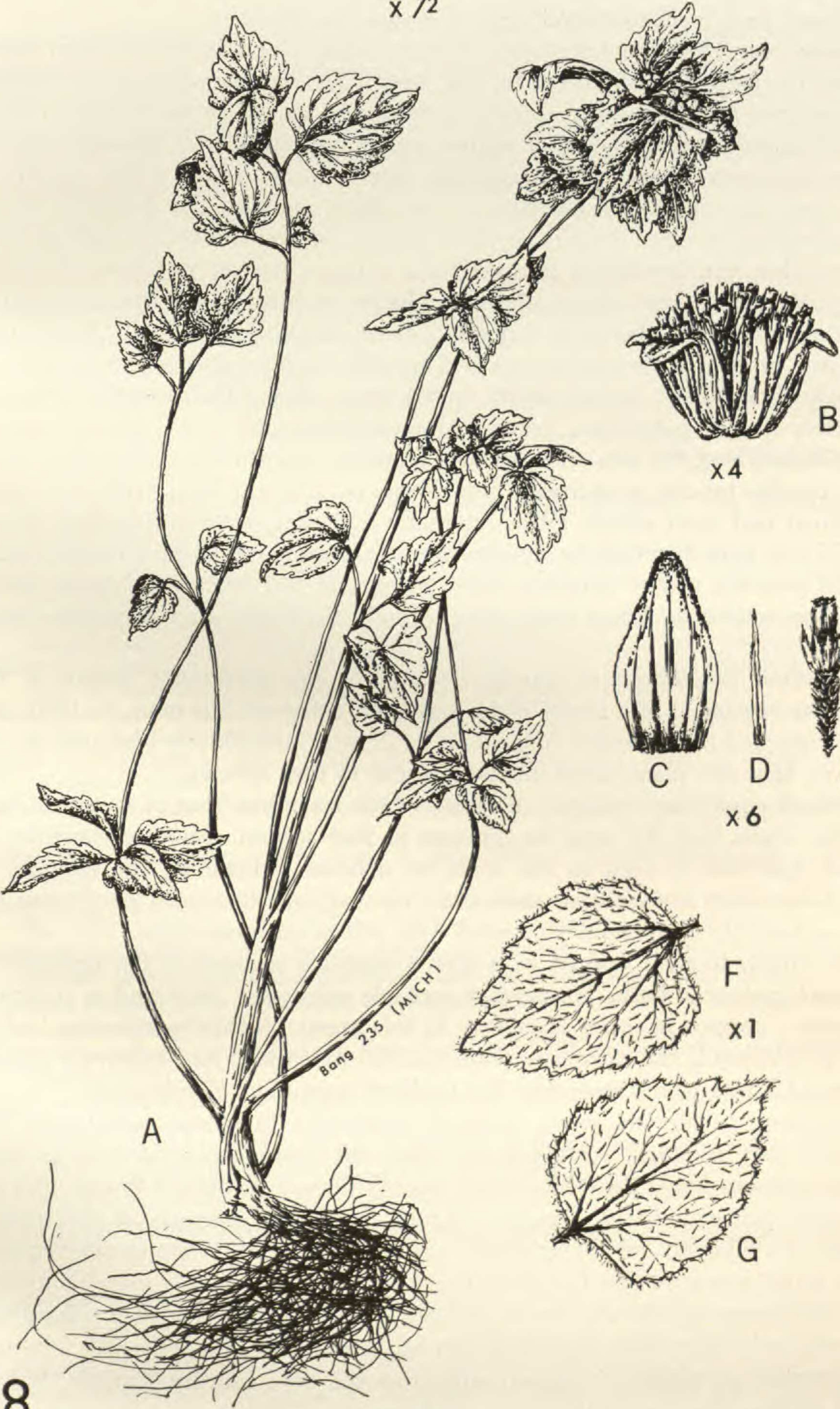
Perennials 3.5–5.5 dm tall; roots coarse, fibrous; stems woody, erect, usually clumped from a woody caudex, simple to branched near inflorescences, bark brown-gray to deep red apically, white pilose-puberulent to pilose-scabrous, at times quite densely so, to becoming subglabrous near upper branches; leaves opposite, remote from inflorescences, petioled, somewhat thick and fleshy, velvety, lanceolate to lanceolate-elliptic, (2.7–)3.1–4.4 cm long, 1.1–1.4 cm wide, base cuneate-attenuate, entire, margin revolute, crenate, becoming entire toward apex, scabrous-puberulous, often deep purplish, apex acute, upper surface yellow-green to dark green, often tinged with purple, conspicuously white pilose, becoming scabrous marginally, venation inconspicuous, lower surface yellow-green,

→

FIGURE 12. *Ageratum guatemalense*. — A. Habit. — B. Inflorescence. — C. Single flower showing the achene and coroniform pappus. — D. Involucral bracts. — E. Detail of upper leaf surface. — F. Detail of lower leaf surface. [After Ownbey & Muggli 3972.]



x 1/2



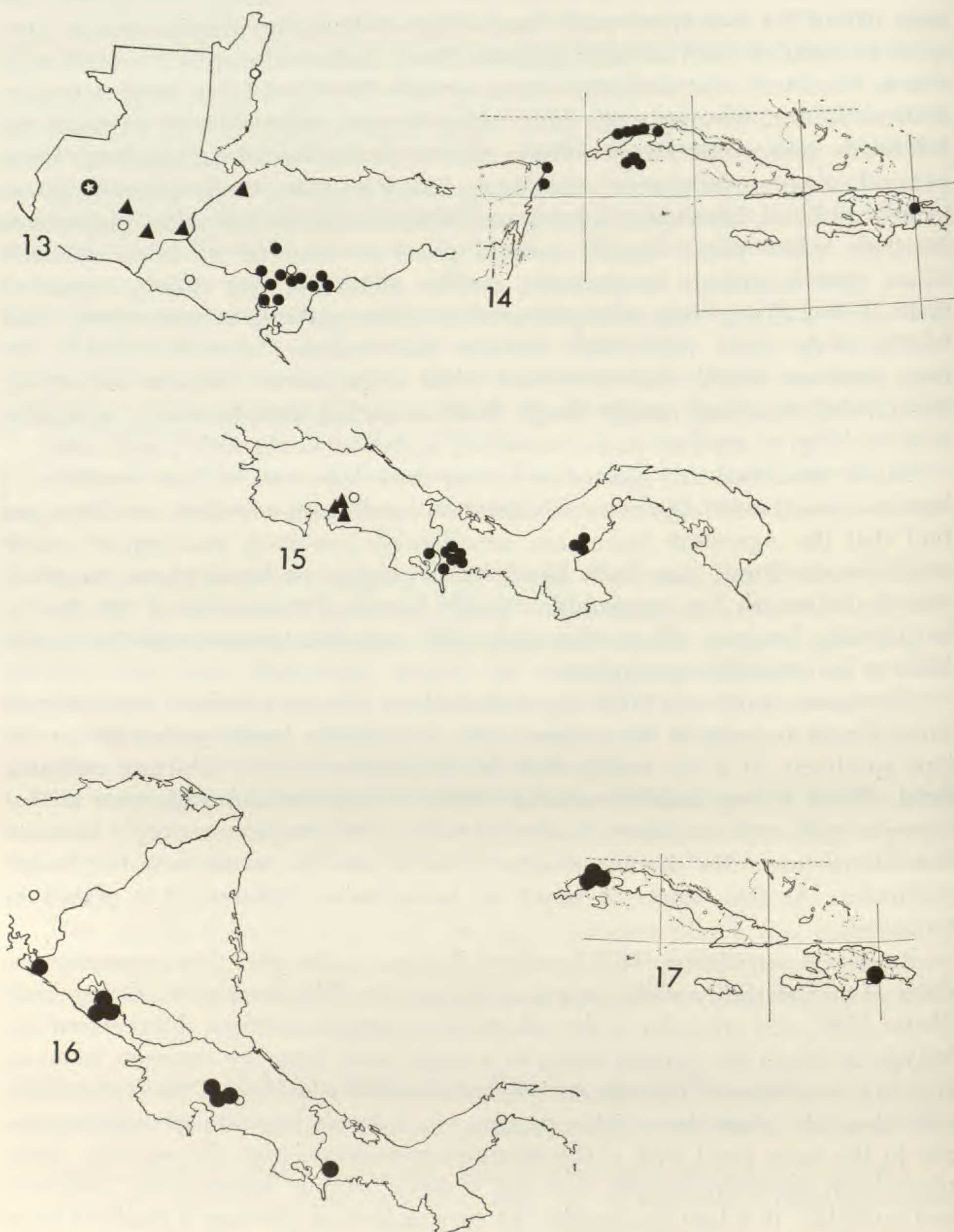
leaves more or less fleshy, petioled, deltoid-ovate to oblong, (0.7–)1.3–2.7 cm long, (0.5–)1.7–1.9(–2.1) cm wide, base obtuse to truncate, margin crenate, apex acute to rounded, both surfaces glabrous, lower surface obscurely 3-nerved, mid-vein at times with scattered white hairs; *petioles* 0.3–1.5(–2.1) cm long, channeled in cross section, bearing white hairs along margin; *inflorescences* terminal, the 2–5 heads grouped in a corymbiform cluster; *peduncles* 0.5–4.2 cm long, finely puberulous-pilose; *involucres* hemispheric, bracts biseriate, rarely triseriate, prominently 2-ribbed, lanceolate, 3.2–4.2 mm high, 0.5–0.9(–1) mm wide, glabrous to sparingly white pilose basally, margin green or scarious, at times minutely ciliate, apex acuminate to attenuate; *corollas* tubular or very slightly expanded, (1.45–)1.75–2.05 mm long, tube pale green or white, glabrous or puberulous, lobes bluish, rarely white, puberulous; *achenes* dark brown, (1.3–)1.45–1.7(–1.8) mm long, glabrous, slightly curved toward white carpodium; *pappus* coroniform, 0.2–0.5(–0.7) mm long, margin deeply laciniate and at times pectinate, appearing as if made up of separate scales, or merely undulate, rarely with 1 or 2 setae.

Kunth described this species as having thick leaves as in *Beta maritima*. I have compared dried specimens of *Ageratum maritimum* with *Beta maritima* and find that the *Ageratum* leaves are considerably less thick and appear nearly membranous. Kunth may have based his description on living plants, in which case the leaves may be comparable. Kunth described the corollas of this species as glabrous; however, observation under 15× magnification revealed the corolla lobes to be externally puberulent.

Ageratum maritimum HBK var. *intermedium* (Hemsl.) Robins. was assigned varietal rank because of the pappus setae and slightly longer peduncles on the type specimen. It is my feeling that this disposition is quite arbitrary and artificial. There is considerable variation within a single head on this type so that a pappus with setae sometimes is adjacent to the more conspicuous deeply laciniate coroniform type. No positive diagnostic value can be ascribed to the longer peduncles. As this variety is based on inconclusive evidence, it is placed in synonymy.

Ageratum maritimum HBK f. *calvum* Robins. is also placed in synonymy because of the variability of the pappus in this species. The description, drawn from Shafer 1099, calls attention to the calvus, i.e., epappose, achenes. I have seen the isotype in which the pappus varies in a single head from the common laciniate type to a mere crown. The pappus is never completely lacking on the fruit. Other collections also show the variable pappus, i.e., a deeply laciniate coroniform pappus in the same head with a coroniform, non-laciniate one. To separate those plants with the entire pappus from the laciniate pappus becomes very arbitrary and artificial. It is best to consider the pappus here as showing a gradient from the very short ones ca. 0.1–0.2 mm long on one extreme and ranging to the opposite extreme where the pappus is to 0.7 mm long, deeply laciniate and, at times, setiferous.

Ageratum maritimum is distinguished by the combination of its creeping decumbent habit, deltoid-ovate to oblong, somewhat fleshy leaves, pilose nodes and coastal sand habitat. As *Ageratum maritimum* and *A. littorale* occupy similar habitats, though they are not known to occur sympatrically, they may be con-



FIGURES 13-17. — 13. The distribution of *Ageratum guatemalense* in Guatemala, *Ageratum chortianum* in Guatemala and Honduras, and *Ageratum standleyi* in Honduras. Circle with star, *A. guatemalense*; solid circle, *A. standleyi*; triangle, *A. chortianum*. — 14. The distribution of *Ageratum maritimum* in Quintana Roo, Cuba, and Hispaniola. (Base map copyright University of Chicago.) — 15. The distribution of *Ageratum oerstedii* in Costa Rica and *Ageratum riparium* in Panama and Costa Rica. Triangle, *A. oerstedii*; solid circle, *A. riparium*. — 16. The distribution of *Ageratum petiolatum* in Panama, Costa Rica and Nicaragua. — 17. The distribution of *Ageratum domingense* in Cuba and Hispaniola. (Base map copyright University of Chicago.)

fused in the herbarium. *Ageratum maritimum* usually has a longer, laciniate pappus that appears to be made up of scales compared to the coroniform type in *A. littorale*, and it is generally more pilose and more fleshy than *A. littorale*. There is a tendency for the heads to be single on an elongated peduncle in *A. maritimum* so that it may resemble *A. gaumeri*. However, the distinctions listed above will separate these species readily.

This species occurs on beaches and limestone near beaches in Cuba, Hispaniola, and islands off Quintana Roo (Fig. 14). Flowers and fruits are present the year around.

CUBA. Bay of Mariel, Britton & Gager 7551 (F, NY, US); Isle of Pines, Britton *et al.* 14930 (F, GH, NY, US); sand banks near the sea near Havana, Curtiss 650 (BM, F, GH, K, MIN, MO, NY, US); back of spray zone on low coralline limestone terrace, Punta Barlovento, N of Mariel, Sauer 1789 (WIS); Old Fort to Punta Barlovento, Shafer 1099 (BM, F, GH, NY, US); Mariano, van Hermann 447 (BM, F, NY, US); without locality, Wright 1631 (BM, F, GH, K, MO).

DOMINICAN REPUBLIC. VEGA: Cotuy, Abbot 749 (US).

MEXICO. QUINTANA ROO: Cozumel Island, Gaumer 93 (GH, K); Isla Mujeres, Sauer & Gade 3238 (WIS); Cozumel Island, Steere 2984 (MICH).

20. *Ageratum littorale* Gray, Proc. Amer. Acad. Arts 16: 78. 1880.

Lectotype: UNITED STATES. Florida: Key West, Bennett s.n. (GH); isotype, NY.

Perennial herb (1.5–)2–5(–7) dm tall; roots coarse, fibrous, at times adventitious at lower nodes; stems somewhat succulent, decumbent to erect, abundantly branched from base, branches opposite, erect, surface deep red to pale green, glabrous to sparsely tomentose at least at nodes, leafy at base, leafless toward inflorescences; leaves opposite, long petioled, thin though somewhat succulent, ovate to deltoid, (1.5–)2–4.1(–4.7) cm long, (0.7–)1–3.7 cm wide, base obtuse, entire, apex acute to broadly so, margin crenate, teeth slightly thickened at apex, upper surface green, glabrous to sparingly tomentose especially when young, lower surface very similar, the 3 main veins more conspicuous from beneath; petioles 1–4 cm long, thin, sparingly tomentose near node; inflorescences terminal, the 3–10 heads grouped in tight corymbose clusters; peduncles usually 1 cm or less long, glabrous to tomentose directly beneath involucre, bracteolate; bracteoles alternate, subulate, glabrous to sparingly tomentose; involucre campanulate, bracts bi- to triseriate, outer series firm, 2-ribbed, oblong to lanceolate, (2.75–)3–4(–4.15) mm long, 0.5–0.9(–1.55) mm wide, pale green to brownish, margin green or scarious, basally entire, at times variously erose and scabrous toward the acute apex, surface glabrous to sparingly tomentose usually only basally, at times scabrous apically; corollas narrowly funnelform, 1.15–2.5 mm long, tube and throat tomentose to glabrous, pale green, lobes puberulent to glabrous, blue-purple to bright blue, rarely white; achenes shining black, (1.25–)1.5–1.8 mm long, glabrous, tapering toward white carpopodium; pappus coroniform, 0.05–0.15 mm long, margin entire to variously undulate, plants from islands in Bay of Honduras often with setiferous pappus scales, then pappus 0.25–1.3(–2.25) mm long.

The species can be divided into formae based upon characters of the pappus and to some extent, geography.

1. Pappus coroniform, margin entire to undulate, not setiferous; south Florida, Grand Cayman Island, rarely in the islands of the Bay of Honduras 20a. *Ageratum littorale* f. *littorale*
1. Pappus setiferous, setae to 2.25 mm long; mainly in the islands of the Bay of Honduras 20b. *Ageratum littorale* f. *setigerum*

20a. *Ageratum littorale* Gray forma *littorale*.

Coelestina maritima Torrey & Gray, Flora 2: 63. 1841, fide Robinson (1913b).

Carelia littorale (Gray) Kuntze, Rev. Gen. 1: 325. 1891, fide Robinson (1913b).

Ageratum littorale Gray var. *hondurensense* Robins., Contr. Gray Herb. 42: 468. 1913.
(Holotype: Bay of Honduras, Ruatan Island, Gaumer 1 (B, not seen); photographs, NY, US; isotypes, GH, US; photograph, MIN.)

Ageratum littorale Gray f. *album* Moldenke, Amer. Midl. Naturalist 32: 562. 1944.
(Holotype: UNITED STATES. Florida: Monroe County, Big Pine Key, Moldenke 817a (NY).)

Torrey and Gray (1841) described this species under the genus *Coelestina* Cass. and applied the appropriate epithet *maritima*. Later, Gray (1880) transferred the species to *Ageratum*, but due to the specific name being preoccupied under *Ageratum* by *A. maritimum* HBK, he adopted *A. littorale*.

Robinson's variety, *hondurensense* was proposed to include plants possessing leaves longer and wider than average. It appears that Robinson did not see many specimens and that his decisions were based on minimal data. Personal study of about 40 different collections shows that leaves of Robinson's variety are well within the range of variation in leaf size throughout the species. There are no grounds for retaining taxonomic recognition of *A. littorale* Gray var. *hondurensense* Robins.

Moldenke (1944) described a plant with white florets as forma *album*. As floret color is quite variable in this species and in the genus as a whole, it does not seem taxonomically sound to recognize taxa based only on corolla color.

Ageratum littorale is the only species native in the United States. Its semi-succulent, glabrous nature, and the minute pappus in combination with a coastal habitat set it apart from other taxa.

Ageratum littorale f. *littorale* occurs in beach sand and in thickets along the sea in the Florida Keys, the West Indies, and in islands in the Bay of Honduras. Flowers and fruits are present throughout the year as local conditions permit.

BRITISH HONDURAS. Half Moon Cay, Stoddart 43 (BM).

CUBA. Sand dunes, Corrientes Bay, Pinar del Río, Britton & Cowell 9954 (NY).

GRAND CAYMAN ISLAND. Sand along road side, Georgetown, Kings GC176 (BM); 25 m from sea in low thicket on roughly pitted ironstone shore, between Jacson Point and Southwest Point, Sauer 3285 (WIS).

UNITED STATES. FLORIDA: Indian Key, Bates s.n. (MICH, MSC); Key West, Bennett s.n. (NY), Blodgett s.n. (GH, NY), Chapman s.n. (MO, NY, US), Pollard et al. 12 (BM, F, MIN, NY, US); sand dunes, east end of Key West, Small & Small 4984 (MO, NY); coral soil, Boca Chica Key, Curtiss 1163 (BM, F, GH, MIN, MO, NY, US); dry sandy soil, Lower Marecumbe Key, Moldenke 662 (K, MO, NY).

20b. *Ageratum littorale* Gray forma *setigerum* Robins., Contr. Gray Herb. 42: 468. 1913.

Holotype: Bay of Honduras, Mugeris Island, Gaumer s.n. (B, not seen); isotype, US; photograph, MIN.

Ageratum littorale Gray var. *hondurensense* Robins. forma *setigerum* Robins. Contr. Gray Herb. 42: 468. 1913.

Forma *setigerum* is very similar to forma *littorale*, differing primarily in the presence of a setiferous pappus in the former. *Ageratum littorale* f. *setigerum* occurs mainly in British Honduras but does reach Florida where forma *littorale* is common. Due to the overlap in geographic range and the single character of the pappus which distinguishes these taxa, the status of forma is maintained.

This forma occurs on the offshore islands and cays of British Honduras; it is apparently more rare on the Keys of Florida. Flowering and fruiting occurs year around as local conditions permit.

BRITISH HONDURAS. Stann Creek, Water Cay, *Robertson* 251 (BM); Turneffe Islands, Deadman II Cay, *Stoddart* 130 (US).

UNITED STATES. FLORIDA: Shore of Jewfish Key, *Curtiss* 5446 (MO, NY, P).

21. *Ageratum platypodum* Robins., Contr. Gray Herb. 42: 464. 1913.

Holotype: MEXICO. Jalisco: Guadalajara, *Palmer* 437 (GH); isotypes, BM, NY, US.

Annuals or short-lived perennials 6–9.5 dm tall; *roots* coarse, fibrous, at times adventitious at lower nodes; *stems* simple to branched above, deep red, minutely puberulent; *leaves* opposite at base of stem to alternate above, petioled, ovate, 5–9.5 cm long, 3–6 cm wide, base obtuse, slightly decurrent along petiole, apex obtuse to acute, margin crenate or dentate, scabrous to glabrous, upper surface yellow-green, glabrous or scabrous, lower surface pale green, abundantly yellow glandular-punctate to sparingly so, sparingly white pubescent over the conspicuous reticulate, sometimes red, veins; *petioles* 1–2.2 cm long, slightly winged and flattened, ca. 2.5 mm wide, 3-veined, sparingly pilose on the margin; *inflorescences* terminal, the 4–10 heads grouped in an irregular corymbose cluster; *peduncles* coarse, bracteolate, from ca. 0.75–2 cm long, pilose-puberulent; *bracteoles* linear, 3–6 mm long, marginally sparingly pilose; *involucres* campanulate, bracts bi- to triseriate, firm, green to reddish, 2-ribbed, ribs prominent basally, lanceolate, (5.25–)5.5–6.5 mm long, (0.85–)1–1.35 mm wide, pubescent with irregularly scattered white, pilose hairs, margin entire, ciliate at least apically, apex acute; *corollas* narrowly funnelform, (2.7–)3–3.3 mm long, tube greenish, puberulent, throat greenish, becoming glabrous toward the 5 pale lavender, glabrous lobes; *achenes* 5-angled, 1.5–1.85 mm long, shiny black, minutely and sparingly scabrous on angles, very slightly tapered toward white carpopodium; *pappus* coroniform, (0.3–)0.5–0.7 mm long, tawny, margin finely and irregularly pectinate to dentate.

Robinson (1913b) placed *Ageratum platypodum* in his section *Euageratum* in which he included those species with free pappus scales. None of the specimens available to me for study indicate this relationship—the pappus is coroniform in all cases. Projecting teeth, if present, are basally united into a cup-like pappus. This feature suggests a closer relationship to those species with a similar pappus structure.

The holotype and isotype of *Ageratum platypodum* were distributed as whole plants but mounted with inflorescences of *A. houstonianum* in the upper right-hand corner of the sheet. Characteristics of the pappus, i.e., the 5 elongate basally free setae, as well as the pubescent corolla lobes and shorter, pilose stipitate-glandular, acuminate bracts of *A. houstonianum* set the species apart in this mixed collection.

Ageratum platypodum shows outward similarities to *A. petiolatum*. Ovate leaves borne on elongate petioles are present in both species. However, the distinguishing characters of *A. platypodum*, the large, ovate leaves with reddish veins, borne on wide petioles, and the prominent ribs toward the base of the involucre bracts, set these species apart.

Ageratum platypodum is a tetraploid species. The chromosome number $n = 20$ was determined from buds (voucher Ownbey & Muggli 3941, MIN) and recorded here for the first time.

This species is known only from Jalisco in wet meadows and along road sides in the pine forest zone from *ca.* 1700–2100 m elevation. Flowers and fruits are present in August and September.

MEXICO. JALISCO: Sierra del Tigre, 2 miles NE of Maxamitla, McVaugh 13133 (MICH, US); mountain plateau 4 miles E of Tapalpa, McVaugh 20700 (MICH); low, wet roadside 6.5 miles E of Tapalpa, cytological voucher, Ownbey & Muggli 3941 (MIN); Guadalajara, Palmer 437 (BM, GH, NY, US).

22. *Ageratum riparium* Robins., Contr. Gray Herb. 42: 473. 1913.

Holotype: COSTA RICA. In arenosis secundum flumen Ceibo, Pittier 4914 (GH).

Ageratum rivale Robins., Contr. Gray Herb. 61: 3. 1920, *non Ageratum rivale* Ses. & Moc., La Naturaleza, ser. 2, app. 1: 136. 1887. (Holotype: PANAMA. Chiriqui Prov.: Vicinity of El Boquete, Maxon 5240 (US); isotype, GH.)

Ageratum panamense Robins., Contr. Gray Herb. 104: 4. 1934.

Annuals or short-lived perennials; *roots* fibrous, commonly adventitious at stem base; *stems* repent to erect, (1.5–)3–4.6(–8.4) dm tall, branched, branches often vertical or ascending, surface dark red above to brown, glabrous below, becoming puberulous to pilose-puberulous toward apex; *leaves* opposite below to alternate above, petioled, ovate to lanceolate, (1.1–)2.5–6.5(–8) cm long, 0.7–2.4(–2.9) cm wide, base obtuse to oblique, entire, apex acute, margin dentate to more or less wavy, upper surface bright green, scabrous to glabrous, puberulous over veins, lower surface pale green, orange glandular-punctate, scabrous at least over the 3 larger veins, to nearly glabrous; *petioles* 0.1–0.5(–1) cm long, pilose; *inflorescences* terminal, the 3–7 heads in an irregular corymbose cluster, rarely borne singly; *peduncles* usually less than 1.5 cm long when in a cluster, to 6 cm long if head solitary, densely pilose-puberulent, bracteolate; *bracteoles* alternate, leaf-like, green to reddish, linear, to 0.5 cm long, pilose to scabrous; *involucres* campanulate, spreading with age, bracts biseriate, 2-ribbed, firm, green to deep red, lanceolate, 4.2–6(–6.85) mm long, (0.7–)1–1.3 mm wide, sparingly pilose at least over the rather prominent ribs to glabrous, margin entire, green to scarious, ciliate at least apically, apex acute, white tipped, at times becoming spine-like; *corollas* funnelform, (2–)2.4–3(–3.75) mm long, tube and throat white to greenish, glabrous, lobes purple to lavender, sparingly pilose; *achenes* dark brown to black (1.5–)2–2.35(–2.8) mm long, glabrous, curved and tapering toward white carpopodium; *pappus* coroniform, (0.1–)0.2–0.8 mm high, tawny, margin variously dentate to laciniate, at times a tooth elongating into a scabrous, subulate awn, then pappus 2–2.3(–2.65) mm long.

Robinson (1913b) described *Ageratum riparium* on the basis of Pittier's collection of a portion of a single robust branch. Later Robinson (1920) described

TABLE 6. A comparison of *Ageratum riparium* and *A. petiolatum*.

Character	<i>A. riparium</i>	<i>A. petiolatum</i>
Leaves.	Ovate to lanceolate, firm, green beneath, sharply dentate.	Ovate to triangular, thin, pale green to gray beneath.
Petioles.	To 1 cm long.	To 3 cm long.
Involucral bracts.	Glabrous to nearly so, pale green, (0.7–)1–1.3 mm wide.	Short pilose, pale green to reddish, 0.5–0.8 mm wide.
Flowering.	January to March, again July to August.	May to July.
Altitudinal range.	(600–)1200–1400 m.	300–900 m, rarely to 1400 m.

A. rivale with a more complete plant as the holotype. As the epithet *rivale* was previously occupied under *Ageratum* (*A. rivale*, Ses. & Moc.), Robinson (1934) chose the name *panamense* to replace *A. rivale* Robins.

Robinson (1913b) employed the oblique leaf bases as noted on the type of *Ageratum riparium* as an important key character. This feature is evident on the type of *A. rivale* as well, though it is very inconsistent on both specimens. The wide, nearly glabrous, light green involucral bracts are shared by both type specimens. Stem color and pubescence are identical on both types as is the dentate to lacinate coroniform pappus. Measurements of structures on both specimens and on the collections as a whole show obvious similarities. Finally, the location of Pittier's collection in Costa Rica and the remainder of the taxon in adjacent Panama suggests that they are the same entity. Since *A. riparium* Robins., *A. rivale* Robins. and *A. panamense* Robins. are conspecific, the oldest validly published name for the taxon, *A. riparium* Robins. must be adopted.

Ageratum riparium and *A. petiolatum* are the only species of *Ageratum* present in Panama besides the weedy and pantropic *A. conyzoides* subsp. *conyzoides*. Though sharing the same type of habitat in part, i.e., moist banks and slopes, these species are readily separated as summarized in Table 6.

Ageratum riparium is distinguished by the combination of wide, glabrous or nearly glabrous involucral bracts with ciliate margins, the sharply dentate ovate leaves, and its moist habitat.

This species is endemic to Panama and adjacent Costa Rica in pastures, wet meadows, and along bogs and river banks from ca. 700–1400 m elevation (Fig. 15). It is in flower from January to March; fruits are present in March. Flowering occurs again in July with fruits present in July and August.

COSTA RICA. Gravien du Rio Ceibo, près du Bornea, Pittier 4914 (GH).

PANAMA. Marsh in valley, El Valle de Antón, Alston 8804 (BM); Boquete, Davidson 590 (F, US); marshy ground and marshes along R. Antón, El Valle de Antón, Hunter & Allen 377 (BM, K); along Río Caldera S of El Boquete, Killip 3612 (US); meadow, El Valle de Antón, Maurice 773 (US); pasture below Alto Lino, Maurice 874 (US); along wet bank of brook, vicinity of El Boquete, Maxon 5240 (US); Boquete, Pittier 2905 (US); Ilano del volcán, Seibert 342 (GH, US); El Valle de Antón and vicinity, Seibert 472 (GH, MIN, NY, US); near El Volcán, White 222 (GH, US); vicinity of Boquete, Woodson & Schery 734 (GH); Finca Lerida to Boquete, Woodson et al. 1102 (GH, NY), Woodson et al. 1147 (GH, US); between Las Margaritas and El Valle, Woodson et al. 1767 (GH, NY, US).

23. *Ageratum oerstedii* Robins., Contr. Gray Herb. 42: 472. 1913.

Coelestina latifolia Benth. in Oersted, Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn. 1852: 71. 1852. (Holotype: COSTA RICA. Monte Aguacate, *Oersted* 251 (K); isotype, C; photograph, GH, fide Robinson (1913b).)

Ageratum latifolium (Benth.) Hemsl., Biol. Centr. Amer. Bot. 2: 82. 1881, non Cav. (1797), fide Robinson (1913b).

Carelia latifolia (Benth.) Kuntze, Rev. Gen. 1: 325. 1891, fide Robinson (1913b).

Annual 3–5(–6.6) dm tall (*cf.* Robinson, 1913b; Standley 1938); *roots* fibrous, at times adventitious at basal nodes; *stems* erect, branched, puberulous and long white pilose, bark mottled deep red and green; *leaves* opposite, long petioled, semi-membranous, widely ovate (5.4–)7–9(–13) cm long, (3.6–)6.5–9 cm wide, base cordate to truncate, entire, slightly decurrent along petiole, margin ciliate, crenate, apex acute, upper surface bright green with widely scattered white pilose hairs, lower surface pale green, abundantly dotted with yellow glandular atoms and white pilose over the conspicuous palmate venation; *petioles* (1–)2.5–4(–6) cm long, white pilose, slightly winged distally; *inflorescences* terminal on stems and branches, numerous heads in loose corymbose clusters; *peduncles* ca. 3–7 mm long, white puberulent, bracteolate; *bracteoles* 1.5–3.5 mm long, subulate, pale green, glabrous, merging with the involucre bracts; *involucres* campanulate, bracts biseriate, 2-ribbed, pale brown at base, becoming pale green above, lanceolate, (3–)4–4.25 mm high, (0.7–)0.8–0.9 mm wide, glabrous, margin entire, scarious, glabrous to ciliate toward acute apex; *corollas* funnelform, (2–)2.25–2.5 mm long, glabrous throughout, tube and throat pale green to white, lobes lavender; *achenes* dark brown to black, 1–1.35(–1.5) mm long, glabrous, slightly tapered toward white carpopodium; *pappus* coroniform, 0.15–0.2 mm high, margin entire to minutely dentate.

This species was described by Bentham and Oersted (1852) under the genus *Coelestina* Cass., and the epithet *latifolia* was applied. Hemsley (1881) transferred *C. latifolia* to *Ageratum* and retained Bentham's epithet, apparently unaware of Cavinille's use of the same epithet in 1797. Robinson (1913b), noting that the epithet *latifolium* was preoccupied under *Ageratum*, published *A. oerstedii*, honoring the collector of the type.

Ageratum oerstedii is poorly represented in herbaria and thus not well known. Nevertheless, the data suggest that *A. oerstedii* is distinct. The combination of large, ovate, membranous leaves with yellow glandular atoms beneath and the pale green, lanceolate, glabrous involucre bracts is common only to this taxon.

Ageratum oerstedii is endemic to Costa Rica (Standley, 1938) in mountains at ca. 600 m elevation (Fig. 15). Plants collected in November and December are in flower and fruit.

COSTA RICA. Del Cacao de Alajuela, *Brenes* s.n. (NY), *Brenes* s.n. (NY); 25 miles E of Punta Arenas, *Cronquist* 8840 (MICH, NY); *Orotina*, *Holway* 324 (GH, MIN); Aguacate, *Oersted* 251 (C, K); without locality, *Oersted* 253 (K). Reported from San Ramon (Robinson, 1913b; Standley, 1938).

24. *Ageratum petiolatum* (Hook. & Arn.) Hemsl., Biol. Centr. Amer. Bot. 2: 83. 1881.

Caelestina petiolata Hook. & Arn., Bot. Beechey Voy. 433. 1841, fide Robinson (1913b). (Holotype: NICARAGUA. Realejo, *Sinclair* s.n. (K); photograph, GH.)

- Coelestina scabriuscula* Benth. ex Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn. 1852: 72. 1852. (Holotype: COSTA RICA. El Veijo, Oersted 250 (C).)
Carelia petiolata (Hook. & Arn.) Kuntze, Rev. Gen. 1: 325. 1891, fide Robinson, 1913b.
Carelia scabriuscula (Benth.) Kuntze, Rev. Gen. 1: 325. 1891.
Ageratum scabriusculum (Benth.) Hemsl., Biol. Centr. Amer. Bot. 2: 83. 1881.

Annual or longer lived, 2.5–5.6(–7) dm tall; *roots* fibrous, rarely adventitious at lower nodes; *stems* simple or sparingly branched, erect, surface reddish to green when young, becoming brownish, white puberulous on upper parts and lower nodes, glabrous or nearly so toward basal internodes; *leaves* opposite, petioled, rather thin, ovate to triangular, 3–6.6(–9) cm long, 1.4–3.8(–4.15) cm wide, base obtuse to very slightly cordate, entire, apex acute, margin crenate, sometimes revolute, upper surface shiny, green, pilose to puberulent and pilose at least over veins, at times yellow glandular-punctate, at times scabrous near margin, lower surface dull, pale green to gray, yellow glandular-punctate, sparingly pilose over the conspicuous reticulate veins; *petioles* (0.7–)1.2–3 cm long, pilose-puberulous marginally; *inflorescences* terminal, the 3–7 or rarely more heads in corymbose clusters; *peduncles* ca. 0.5–3 cm long, densely white puberulent-pilose, bracteolate; *bracteoles* alternate, linear, puberulent-pilose, to ca. 5 mm long, merging with involucre; *involucres* campanulate, bracts biseriate, 2-ribbed, firm, pale green to reddish, lanceolate, (3.5–)4–4.85 mm long, 0.5–0.8 mm wide, sparingly pilose at least basally, becoming glabrous apically, margin entire, glabrous to ciliate, apex acute; *corollas* funnellform, 2.25–3 mm long, glabrous throughout, tube and narrowly expanded throat greenish, lobes and style branches lavender; *achenes* glistening black, 1.45–2 mm long, glabrous, slightly tapering toward white carpopodium; *pappus* coroniform, white, 0.15–0.5 mm long, margin variously dentate, at times with a single subulate, scabrous awn to 2.5 mm long.

The type locality of *Ageratum petiolatum* is given as Realejo, Guatemala, by Hooker and Arnott (1841) who also list the location at 12° 45' N. Modern maps show this latitude to be within Nicaragua. Robinson (1913b) was aware of the correct locality, and listed the type from Nicaragua.

Comparing the type specimens of *Ageratum scabriusculum* and *A. petiolatum* readily shows them to be conspecific. Robinson, apparently, was of the same opinion. He placed the penciled note "the type material of *A. scabriusculum* (Benth.) Hemsl. is just this sort of smoothish thing, clearly identical. B. L. R. 1925" on Wright s.n. (GH). Both possess the characteristics of *A. petiolatum*, namely nearly glabrous, thin, long petioled, ovate leaves which are pale green to gray beneath. The binomial *A. petiolatum* (Hook. & Arn.) Hemsl., published eleven years before *A. scabriusculum* (Benth.) Hemsl., must be adopted for this species.

The chromosome number $n = 10$ was determined from meiotic material of King 5289 but published (Turner & King, 1964) as *A. corymbosum*. Study of the voucher leaves no question but that it should be referred to this taxon.

This species occurs from Nicaragua (Guatemala?) to Panama in moist habitats on slopes and along road sides from ca. 300–900 m elevation, uncommon to 1400 m (Fig. 16). Flowers are present from May through July; fruits are present from July through September(–January).

COSTA RICA. De la route a Alta Río Jesús en San Ramón, *Brenes* 3542 (F, NY); vicinity of San Ramón, *Brenes* 4350 (F, NY); "La Calera" de San Ramón, *Brenes* 6435 (F); Cerro de San Isidro, *Brenes* 14494 (GH); San Miguel de San Ramón, *Brenes* 14930 (F); San Juanello, *Smith* 9818 (F).

NICARAGUA. Managua, *Artemio* 70 (US); Masaya, *Baker* 2220 (GH); Sierra de Managua, *Garnier* 199 (US); slope of Santiago Volcano near Masaya, *Maxon* 7661 (GH, US); Las Nubes and vicinity S of Managua, *Maxon et al.* 7464 (US); El Vieja, *Oersted* 250 (C); Realejo, *Sinclair* s.n. (K); vicinity of Casa Colorado near El Curcero, summit of Sierra de Managua, *Standley* 8188 (F, GH); without locality, *Chaves* 335 (F, US), *Wright* s.n. (GH, US).

PANAMA. 25 miles N of Concepción, cytological voucher, *King* 5289 (TEX, UC); without locality, *Oersted* s.n. (BM).

25. *Ageratum lucidum* Robins., Proc. Amer. Acad. Arts 36: 475. 1901.

Holotype: MEXICO. Morelos: On mossy sides of conglomerate knobs of Sierra de Tepoxtlán, 7500 ft., *Pringle* 8362 (GH); isotypes, BM, C, F, K, MICH, MIN, MO, MSC, NY, P, UC, US.

Perennial *shrubs* 3-5(-8.5) dm tall; *roots* fibrous; *stems* erect, finely striate, branched, branches opposite, usually curved, ascending, younger parts reddish, older bark gray, densely white puberulous with scattered orange glandular atoms at least on younger parts to glabrous or nearly so on older, leafy nearly to inflorescences; *leaves* opposite, petioled, firm, ovate, 3-5(-7) cm long, 1.6-2.2(-4) cm wide, base obtuse, apex acute, margin slightly revolute, scabrous, serrate, teeth white tipped, to entire, upper surface bright, shining green, orange-glandular punctate, sparingly white puberulous at least over the prominent reticulate veins, lower surface shiny, pale green, densely orange glandular-punctate, sparingly puberulous over the conspicuous venation; *petioles* 0.4-1 cm long, very narrowly winged, adaxially channeled, puberulous with scattered orange glandular atoms; *inflorescences* terminal, heads 0.6-0.9(-1) cm in diameter, solitary or 3-7 grouped in an irregular, corymbose cluster; *peduncles* 0.5-3.6 cm long, often subtended by opposite, linear-lanceolate, green, reduced leaves, bracteolate, densely puberulous with scattered, glandular atoms; *bracteoles* alternate, narrowly linear, puberulous, glandular-atomiferous, about 5 mm long, merging with involucre; *involucres* campanulate, bracts biseriate, firm, 2-ribbed, prominently so basally, outer bracts lanceolate to lance-oblong, rarely linear, (4.75-)5-6(-6.25) mm long, 0.75-1.1(-1.8) mm wide, green throughout to vari-ously tinged with reddish-purple, white puberulous with orange glandular atoms basally, less puberulous toward apex, margin entire, green or scarious, at times ciliate, apex acute, inner bracts similar though less puberulous; *corollas* funnel-form, (2.25-)2.5-3 mm long, orange-glandular atomiferous, sparingly puberulous or glabrous, white (?); *achenes* 5-angled, shiny, black, (1.35-)1.5-2.2(-2.5) mm long, glabrous, slightly tapered toward white carpopodium; *pappus* coroniform, white, (0.2-)0.3-0.5 mm long, margin shallowly dentate, rarely producing a single subulate awn, then pappus 2-3.1 mm long.

Ageratum lucidum, an attractive shrubby species, is apparently rare and local in its distribution. All specimens, except one, available for study were collected from the same location by Pringle, most recently in 1906. The most distinctive characteristics are the very bright and shiny green leaves, the short shrubby habit, and the heads which are somewhat larger than in other species.

Ageratum lucidum is seemingly restricted to Sierra de Tepoxtlan, Morelos, and eastern Jalisco. Buds, flowers and fruits were noted on specimens collected from August to November.

MEXICO. JALISCO: Near farm land, 42 miles E of Guadalajara, *Waterfall* 15638 (MICH). MORELOS: Sierra de Tepoxtlan, *Pringle* 8362 (BM, C, F, K, GH, MICH, MIN, MO, MSC, NY, P, UC, US), *Pringle* 13022 (F, GH, K, MICH, MO, MSC, UC, US), *Pringle* 13805 (F, MICH, MO, MSC, UC, US).

26. *Ageratum scorpioideum* Baker in Mart., Fl. Bras. 6(2): 197. 1876.

Holotype: BRITISH GUIANA. Rob. Schomburgk 353 (K).

Perennial (?) herbs; roots coarse, fibrous, adventitious at nodes and internodes; stems erect or repent, branched, branches erect, 3–4 dm tall, deep reddish, glabrous throughout, leafy nearly to apex; leaves opposite, very short-petioled to sessile, lanceolate, 5–8 cm long, 1.3–1.7 cm wide, base entire, gradually acuminate, apex acute, margin crenate on distal $\frac{3}{4}$, upper surface glabrous, inconspicuously pinnately veined, lower surface glabrous, conspicuously pinnately veined; petioles, if present, glabrous, less than 4 mm long; inflorescences terminal, the solitary heads grouped in an irregular panicle; peduncles glabrous, 0.2–1 cm long, bracteolate only at nodes; bracteoles semi-membranaceous, keeled, ca. 2 mm long; involucre campanulate, bracts biseriate, inconspicuously 2-ribbed, outer series lanceolate, 2.6–3 mm long, 0.9–1.15 mm wide, glabrous to very sparingly short pilose, apex acute, margin entire, glabrous to sparingly ciliate, inner series spatulate; corollas funnelform, 1.1–1.3 mm long, glabrous throughout, tube ca. 0.25 mm long, abruptly expanded into the throat; achenes dark brown, glabrous, 1.2–1.5 mm long, contracted apically, slightly tapered toward inconspicuous carpodium; pappus coroniform, 0.3–0.5 mm high, margin 5-dentate.

Some confusion exists as to the correct designation of a type specimen for this species. Three different collections are referred to as the type on herbarium labels, namely Schomburgk 353, 355, and 1188. The only specimen cited in the original description of *Ageratum scorpioideum* is Schomburgk 353. I have seen this specimen at Kew, and since it is the only one cited by Baker it should automatically become the holotype. Schomburgk 355, also at Kew, bears a label reading "Type Specimen." And although it was presumably seen by Baker, it can hardly be accepted as type. Schomburgk 1188 is designated on the label as the type for *Coelestina repens* Sch. Bip., a *nomen nudum* listed in Schomburgk (1848). Though Schultze's name is older, its publication is not valid, and it cannot be applied.

Ageratum scorpioideum is a poorly known species, and apparently it has not been collected since Schomburgk obtained it in 1842. Nevertheless, the limited material available shows a distinctive species separated from all others by the combination of glabrousness, the very small, paniculate heads, and the sessile, lanceolate leaves.

This species is known only from moist savannahs in British Guiana. No dates of flowering or fruiting are known.

BRITISH GUIANA. Moist savanne, Canuku Mountains, Richard Schomburgk 488 (GH, P); Savanne, Richard Schomburgk 1188; photograph (F, TEX), specimen at (B) undoubtedly

destroyed during World War II; Pirara, *Robert Schomburgk* 355 (BM, K, MO); without locality, *Robert Schomburgk* 353 (K).

Section III. **Pectinellum** DC., Prod. 5: 109. 1836.

Annuals; roots fibrous and adventitious at nodes; *stems* repent; *leaves* opposite, on long vertical petioles, cordate-orbiculate, margin lobed $\frac{1}{3}$ – $\frac{1}{2}$ way to midline of leaf; *inflorescences* borne singly; *involucral bracts* biseriate, oblong to spatulate, pilose, unribbed; *corollas* pale lavender to white, abruptly expanded into the campanulate throat; *achenes* glabrous, carpopodium very small or lacking; *pappus* of free oblong tan scales apically fimbriate to short setiferous.

The single species of this section is confined to moist habitats in Cuba and Hispaniola. Data concerning flowering and fruiting is incomplete and inconclusive.

Type species: *Ageratum domingense* Spreng.

27. **Ageratum domingense** Spreng., Syst. 3: 446. 1826.

Holotype: SANTO DOMINGO. Without specific location, *Bertero* s.n. (DC-G, not seen); isotype, P; photograph, US; tracing, GH.

Phania domingensis (Spreng.) Griseb., Cat. Pl. Cub. 145. 1866, fide Robinson (1913b).

Carelia domingensis (Spreng.) Kuntze, Rev. Gen. 1: 325. 1891, fide Robinson (1913b).

Eupatorium planellasianum Maza & Molt., Anales Hist. Nat. 29: 271. 1890. *Nomen nudum*, fide Robinson (1913b).

Annual, to 1.5 dm long; roots fibrous, adventitious at nodes; stems green, sparsely branched, repent, white pilose; leaves numerous, opposite, petioled, cordate-orbiculate, 0.5–1.1 cm long, 0.5–1.2 cm wide, margin lobed $\frac{1}{3}$ – $\frac{1}{2}$ way to midline of leaf, lateral lobes oblong, pointing toward apex, apical lobe slightly larger, all lobes entire, apically obtuse, upper lamina surface dark green, lower surface paler, both surfaces white-pilose and glandular-punctate, punctae yellow to amber, the 3 veins inconspicuous from beneath; petioles (0.2–)0.4–1.5(–2.5) cm long, white pilose, vertical along repent stem; inflorescences of a single head borne on pilose-puberulent, bracteolate peduncle, 2.5–4.5 cm long; bracteoles alternate, pilose, ca. 1 mm or less long; involucre turbinate, bracts biseriate, oblong to spatulate, (2–)2.4–3(–3.5) mm high, an outer one 0.6–1(–1.9) mm wide, green to brownish, apex acute or obtuse, surface unribbed, pilose, margin entire; corollas pale lavender to white, (1.25–)1.75–2.2 mm long, glabrous to sparsely dotted with yellow-amber glandular atoms, tube abruptly expanded into the campanulate throat and 5 spreading acute lobes; achenes 1.4–1.5 mm long, glabrous, brown to black, tapering toward sharply acute base; carpopodium very small or absent; pappus of 5 free, oblong, tan scales, 0.4–1 mm long, apically variously fimbriate to short setiferous.

Ageratum domingense is placed in a separate section and is unique in the genus in the following features. It alone possesses trailing, repent stems, ribless involucral bracts, cordate-orbiculate leaves with lobed margins disposed on vertical petioles, and pollen grain exines about 5 μ thick, which is 2–3 μ thicker than observed in other species. That *A. domingense* does belong with *Ageratum* is obvious from the five oblong, flattened pappus scales and anther appendages.

Both *Ageratum domingense* and *A. gaumeri* have the elongated peduncle

bearing a single terminal inflorescence, though I do not believe this common character necessarily indicates a close relationship. *Ageratum domingense* has too many unique features to suggest a close relationship with any species of *Ageratum*.

Ageratum domingense is restricted to river banks and rocky hill sides in Cuba and Hispaniola (Fig. 17). Dates of flowering and fruiting are incomplete, but on the specimens studied, flowers and fruits are present in March, July, and December.

CUBA. PINAR DEL RIO: Vinales, *Alain 4427* (NY); Bahía Honda, *Ekman 10398* (F), *Wilson 9405* (GH, NY); Sierra de les Orgonos, valley of Río Santa Cruz, *Ekman 16401* (NY); banks of Eaco Eaco River, *León 12517* (NY); without locality, *Wright 2798* (K, NY).

HISPANIOLA. Without locality, *Bertero s.n.* (P).

Section IV. *Stachyofolium* M. F. Johnson, sect. nov.

Perennis. Radix fibrata. Folia alterna, elliptica. Capitula formata in corymbum terminalem. Involucra squamis lineari-spatulatis, 4-costate, margine integro. Receptaculum nudum. Corollae infundibuliformes, albae, pilosae et glandulosae. Achenia glabra, basin versus decrecentia, carpopodio carentia. Pappus coroniformis, margine integro vel dentibus exiguis.

Perennials; roots fibrous; leaves alternate, elliptic; inflorescences grouped in a loose corymbose cluster; involucre bracts biseriate, linear to spatulate, 4-ribbed, margin entire; receptacle naked; corollas funnelform, white, pilose and glandular; achenes glabrous, tapering to base, carpopodium lacking; pappus coroniform, margin entire to obscurely dentate.

Data concerning distribution and flowering are incomplete.

Type species: *Ageratum stachyofolium* Robins.

28. *Ageratum stachyofolium* Robins., Proc. Amer. Acad. Arts 36: 476. 1901.

Holotype: MEXICO. Oaxaca: Vicinity of La Parada, *Nelson 991* (GH); isotypes, F, K, US; photograph, MIN.

Perennial, 5.5–6 dm tall; roots coarse, white, fibrous; stems erect, simple, reddish, white pilose throughout, becoming densely so toward inflorescences; leaves alternate throughout or very rarely opposite below and alternate above, sessile or short-petioled, elliptic, 3–3.5 cm long, 1.1–1.4 cm wide, base obtuse, apex widely acute, margin revolute, crenate, teeth slightly thickened, upper surface dark green, white pilose, lower surface pale green, white pilose and mixed with yellow glandular atoms, veins reticulate, prominent; petioles 1–5 mm long, white pilose or absent; inflorescences terminal, the 7–10 heads disposed in a loose corymbose cluster; peduncles ca. 1.5–3 cm long, densely canescent-pilose, bracteolate; bracteoles ca. 1 cm long, filiform to spatulate, white pilose; involucres campanulate, bracts biseriate, firm, 4-ribbed, pale green, linear to spatulate, (5–)6–6.5 mm high, 0.55–0.7 mm wide, margin entire, apex acute, surface white pilose, becoming densely so at apex, at times with scattered yellow glandular atoms; corollas white, funnelform, 3.25–3.55 mm long, the narrow tube and slightly expanded throat white-pilose with scattered glands, lobes glabrous, style branches long exerted ca. 4× corolla in length; achenes brown to black, 2.25–2.7

mm long, glabrous, tapering to pointed base, carpopodium lacking; *pappus* coroniform, tan, firm, 0.35–0.55 mm long, margin entire to obscurely dentate.

Ageratum stachyofolium is poorly represented in herbaria and is not well known. However, characteristics of the pappus in particular and of the inflorescences in general place the species in *Ageratum*.

The combination of the oblong, 4-ribbed involuclral bracts, the sharply pointed achene lacking a carpopodium, and the alternate leaves is unique in the genus and suggests that *A. stachyofolium* is only distantly related to the other species of *Ageratum*. Thus it is disposed in a separate section. The affinities of *A. stachyofolium* may become more clear when a greater abundance of specimens is available for study.

This species is known only from the type locality, La Parada, Oaxaca, at ca. 2500–2800 m elevation. I have been unable to find this site on the maps I consulted. Plants studied were collected in August and were in flower and fruit.

Section V. *Perplexans* M. F. Johnson, sect. nov.

Herba annua. Radix fibrata. Folia opposita, deltata vel rhombea. Capitulis in cymas formatis. Involucra squamis sub-membranaceae, 5-nervatis, ovatae, margine integro. Receptaculum paleaceum. Paleae sub-membranaceae, lanceolatae. Corollae anguste infundibuliformes, scabrisque. Achenia paginae scabris pilis luteis; carpopodio non manifesto. Pappus 5–6 squamis lanceolatis, membranaceis.

Annual *herbs*; *roots* fibrous; *leaves* opposite, deltoid or rhomboid; *heads* grouped into cymose clusters; *involuclral scales* sub-membranaceous, 5-nerved, ovate, margin entire; *receptacle* paleaceous, paleae sub-membranaceous, lanceolate; *corollas* narrowly infundibuliform, scabrous externally; *achenes* coated with scabrous yellow upward pointing hairs, the carpopodium inconspicuous; *pappus* of 5–6 lanceolate, membranaceous scales.

The single species in this section is known only from Yungas, Bolivia. Dates of flowering and fruiting are not known.

Type species: *Ageratum perplexans* M. F. Johnson.

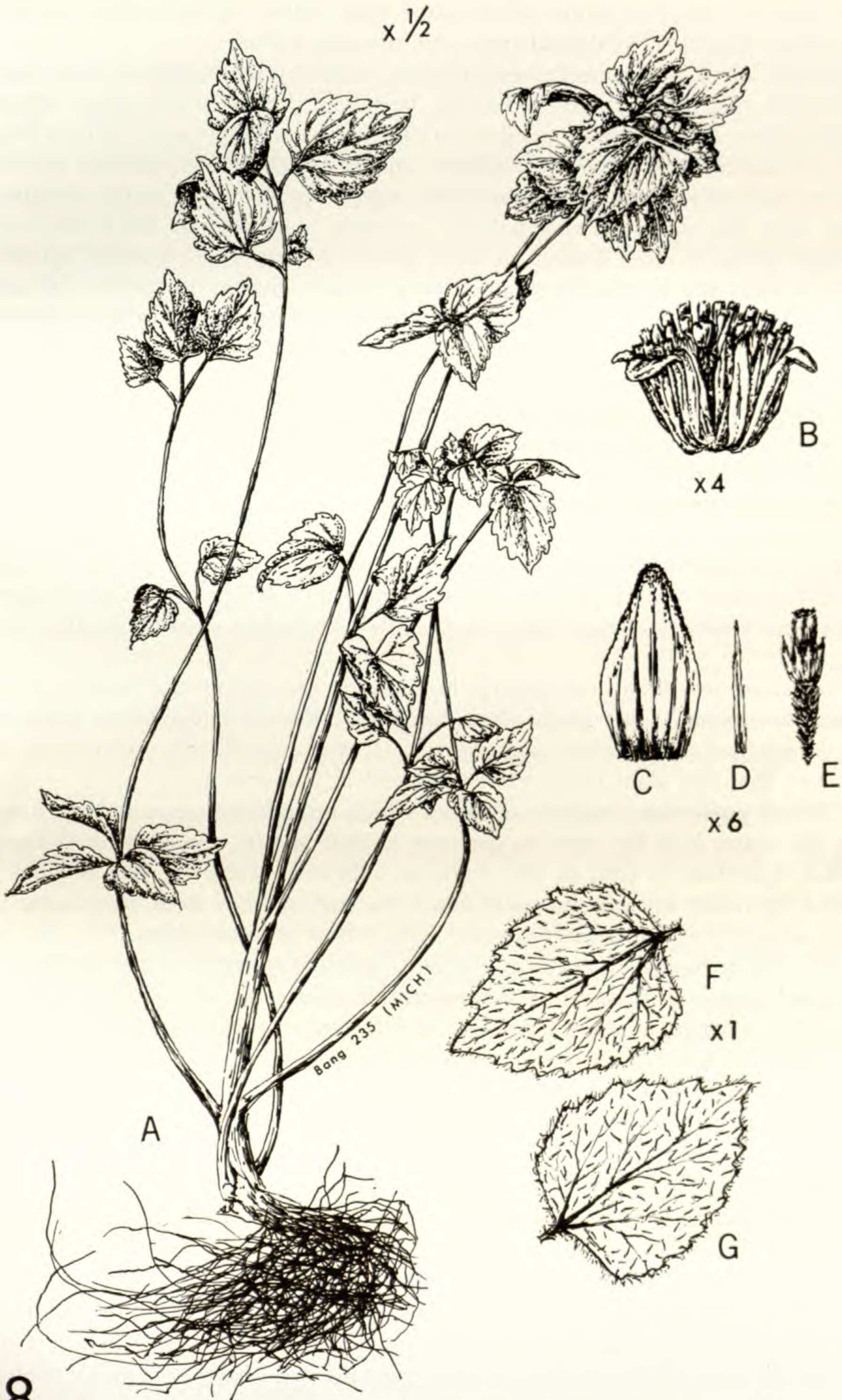
29. *Ageratum perplexans* M. F. Johnson, sp. nov.

Holotype: BOLIVIA. Yungas, 1890, A. Miguel Bang 235 (MICH); isotype, NY. Distributed as *Ageratum conyzoides* L.

Involucra hemisphaerica. Squamae 3-seribus submembranaceae, 5–6 nervis non manifestis, ovatae, 3.25–3.5 mm altae, 2–2.25 mm latae, pallide viridulae, purpureae apicem versus et insuper vervis, paginis glabris, rarius sparsissime breviter pilosae, marginem versus herbae naturam habentes, margine integro, apice ciliato, late rotundae. Receptaculum conicum, paleaceum. Paleae submembranaceae, 1 vel 2 nervis, lanceolatae, ca. 2.75 mm longae, ca. 0.5 mm latae,

→

FIGURE 18. *Ageratum perplexans*. — A. Habit. — B. Inflorescence. — C. Involuclral bract. — D. Receptacle palea. — E. Flower with scabrous achene and pappus scales. — F. Detail of lower leaf surface. — G. Detail of upper leaf surface. [After Bang 235.]



paginis glabris, margine aliquantulum eroso, apice acuto. Achenia nigra, paginae acheniorum scabris pilis luteis. Pappus 5-6 squamis, fulvis.

Annual, ca. 3.5-4 dm tall; *roots* fibrous; *stems* erect, branched from base, glabrous or sparingly puberulent basally, becoming densely white pilose toward inflorescences; *leaves* opposite, deltoid to rhomboid, ca. 3.6 cm wide, 4.5 cm long, apex acuminate, base truncate or obtuse, entire, margin pilose, coarsely crenate to very shallowly lobed, teeth cuspidate, upper surface dark green, sparingly pilose over the inconspicuous palmate venation; *petioles* ca. 2-2.2 cm long, sparingly pilose to more densely so when young; *inflorescences* terminal on stem and branches, the few heads grouped in a cymose cluster; *peduncles* 3-5 mm long, puberulous-pilose, ebracteolate; *involucres* hemispherical, bracts 3-seriate, sub-membranaceous, obscurely 5-nerved, ovate, 3.25-3.5 mm high, 2-2.35 mm wide, pale green, purple over nerves and apically, surface glabrous to rarely very sparingly short pilose, margin entire, herbaceous, apex ciliate, broadly rounded; *receptacle* conical, paleaceous, paleae sub-membranaceous, 1 or 2 nerved, lanceolate, 2.75 mm long, 0.5 mm wide, surface glabrous, margin somewhat erose, apex acute; *corollas* tubular to narrowly funnelform, ca. 1.75 mm long, white (?), tube and throat and short obtuse lobes externally scabrous; *achenes* 5-angled, black, ca. 1.75 mm long, tapering to inconspicuous carpopodium, surface covered with upward pointing yellow scabrous hairs; *pappus* of 5-6 lanceolate, tawny membranaceous scales ca. 1 mm long, margin finely fimbriate, apex fimbriate, acute (Fig. 18).

Ageratum perplexans, so named because of the perplexing nature of the characters combined in a single plant, has been collected but once, in 1890, and was determined as *Ageratum conyzoides* L. It was immediately apparent to me, however, that this plant could not be referred to that species.

Though possessing a pappus of scales which resembles that of section *Ageratum*, the scales lack the setae so common in that section. Another similarity to section *Ageratum* is seen in the scabrous achenes. However, the achenes in section *Ageratum* are scabrous only along the angles, while in *A. perplexans* the entire achene is conspicuously covered with yellow scabrous hairs.

An affinity to some species in section *Coelestina* is noted in the presence of receptacle paleae in both. However, receptacle paleae are not found in combination with a pappus of scales elsewhere in this genus. A third perplexing feature of *A. perplexans* is the extremely wide (to 2.35 mm wide) and relatively smooth involucre bracts which resemble the unribbed ones of *A. domingense*.

Ageratum perplexans shows outward similarities to species which are very probably only remotely related to it. Also, the combination of achenes with yellow scabrous hairs, the wide, ovate, merely nerved involucre bracts, and the receptacle paleae is found nowhere else in the genus. Because of this unique mixture of characters, which suggests a quite remote relationship to other species in the genus, a new section is erected to encompass it. Hopefully more collections of *A. perplexans* will become known so that a more complete study of this strange and extremely interesting *Ageratum* can be made.

Ageratum perplexans is known only from the type locality, Yungas, Bolivia. Dates of flowering and fruiting are not known.

EXCLUDED NAMES

Though I have not personally seen specimens for all the excluded names, I have studied their descriptions and concur with B. L. Robinson's disposition where indicated. Dr. Rogers McVaugh has studied type specimens of several species; I am following his determinations where indicated.

- Ageratum adscendens* Sch. Bip. ex Benth. & Hook., Gen. Pl. 2: 242. 1873, is *Oxylobus adscendens* (Sch. Bip.) Robins. & Greenm. (Robinson, 1913b).
- Ageratum agrianthus* O. Hoffm. in Engler & Prantl, Nat. Pfl. 4(5): 134. 1890, is *Trichogoniam* sp. (Robinson, 1913b).
- Ageratum alternifolium* (Gardn.) Baker in Martius, Fl. Bras. 6(2): 195 is a species dubium (Robinson, 1913b).
- Ageratum altissimum* L., Sp. Pl. 2: 839. 1753, is *Eupatorium urticaefolium* Reichard (Robinson, 1906a; 1906b).
- Ageratum angustifolium* Spreng., Syst. 3: 446. 1826, is *Calea angustifolia* (Spreng.) Sch. Bip. ex Baker in Martius, Fl. Bras. 6(3): 256. 1884.
- Ageratum aquaticum* Roxb., Hort. Bengal. 61. 1814, is *Adenostemma lavenia* (L.) Kuntze, Rev. Gen. Pl. 1: 304. 1891.
- Ageratum arbutifolium* HBK is *Oxylobus arbutifolius* (HBK) Gray (Robinson, 1913b).
- Ageratum callosum* Wats. is *Alomia callosa* (Wats.) Robins. (Robinson, 1913b).
- Ageratum campuloclinioides* Baker in Martius, Fl. Bras. 6(2): 196. 1876, is *Trichogoniam* sp. (Robinson, 1913b).
- Ageratum ciliare* L., Sp. Pl. 2: 839. 1753, is of uncertain application. See discussion under "History of Taxonomic Literature."
- Ageratum coeruleum* Desf., Tab. École Bot. 98. 1804, is a nomen nudum.
- Ageratum coeruleum* Sieber ex Baker in Martius, Fl. Bras. 6(2): 345. 1876, is *Eupatorium macrophyllum* L. (Robinson, 1913b).
- Ageratum confertum* (Gardn.) Benth. ex Baker in Martius, Fl. Bras. 6(2): 195. 1876, is excluded because of the clavellate pappus scales but needs further study (Robinson, 1913b).
- Ageratum conspicuum* Hort. ex C. Koch & Fint, Wochenshr. Gärtnerei Pflanzenk. 1858: 33. 1858, is *Eupatorium glechonophyllum* Less. (Robinson, 1913b).
- Ageratum conyzoides* Sieber ex Steudel, Nom. Bot. Ed. 2. 2: 37. 1841, is *Eupatorium repandum* Willd. (Robinson, 1913b).
- Ageratum corymbosum* (DC.) Benth., Bot. Voy. Sulphur 111. 1844, is *Trichogoniam* sp. (Robinson, 1913b).
- Ageratum corymbosum* Zuccag. var. *st-antonii* Sch. Bip. ex Klatt, Leopoldiana 20: 75. 1884, is a nomen nudum.
- Ageratum febrifugum* Ses. ex DC, Prodr. 5: 104. 1936, is *Piqueria trinervia* Cav. (Robinson, 1913b).
- Ageratum glanduliferum* Sch. Bip. ex Hemsl. in Godman & Salvin, Biol. Centr. Amer. Bot. 2: 82. 1881, is *Oxylobus glanduliferus* (Sch. Bip.) Gray (Robinson, 1913b).
- Ageratum glanduliferum* Sch. Bip. var. *albiflorum* Sch. Bip. ex Gray, Proc. Amer. Acad. Arts 15: 26. 1879, is *Oxylobus glanduliferus* (Sch. Bip.) Gray (Robinson, 1913b).
- Ageratum glaucum* Hort. ex Vilmorin, Blumengärtnerei, Ed. 3. 1: 448. 1894—The description suggests a *Eupatorium*.
- Ageratum guianense* Aublet, Hist. Pl. Gui. Fr. 2: 800. 1775, is *Eupatorium macrophyllum* L. (Robinson, 1913b).
- Ageratum heterolepis* Baker in Martius, Fl. Bras. 6(2): 198. 1876, is *Alomia heterolepis* (Baker) Robins. (Robinson, 1913b).
- Ageratum isocarphoides* (DC.) Hemsl. in Godman & Salvin, Biol. Centr. Amer. Bot. 2: 82. 1881, is *Alomia isocarphoides* (DC.) Robins. (Robinson, 1913b).
- Ageratum laciniatum* Ses. & Moc., La Naturaleza, ser. 2. 1: 136. 1887, is *Stevia trifida* Lag. (personal communication, R. McVaugh).
- Ageratum lasseauxii* Carr., Rev. Hort. 42: 90. 1870, is *Eupatorium lasseauxii* Carr. (Robinson, 1913b).
- Ageratum latifolium* Cav. var. *galapageium* Robins., Contr. Gray Herb. 42: 466. 1913, is *Alomia* sp.
- Ageratum lineare* Cav., Ic. Descr. Pl. 3: 3. t. 205. 1795, is *Palafoxia linearis* (Cav.) Lag. (Robinson, 1913b).
- Ageratum longifolium* (Gardn.) Benth. ex Baker in Martius, Fl. Bras. 6(2): 197. 1876, is *Alomia longifolia* (Gardn.) Robins. (Robinson, 1913b).

- Ageratum matricarioides* (Spreng.) Less., Syn. Gen. Composit. 155. 1832, is *Phania matricarioides* (Spreng.) Griseb. (Robinson, 1913b).
- Ageratum melissaefolium* DC, Prodr. 5: 109. 1836, is *Trichogoniam* sp. (Robinson, 1913b).
- Ageratum microcarpum* (Benth.) Hemsl. in Godman & Salvin, Biol. Centr. Amer. Bot. 2: 82. 1881, is *Alomia microcarpa* (Benth.) Robins. (Robinson, 1913b).
- Ageratum microcephalum* Hemsl. in Godman & Salvin, Biol. Centr. Amer. 2: 82. 1882, is *Alomia microcephala* (Hemsl.) Robins. (Robinson, 1913b).
- Ageratum microphyllum* Sch. Bip. in Seemann, Bot. Voy. Herald 298. 1856, is *Ageratella microphylla* (Sch. Bip.) Gray, Proc. Amer. Acad. Arts 22: 419. 1887.
- Ageratum obtusifolium* Lam., Encycl. Méth. 1: 54. 1783, is not well enough described for proper disposition.
- Ageratum paniculatum* Hort. ex Steudel, Nomen. Bot., Ed. 2. 1: 609. 1840, is *Brickellia paniculata* (Mill.) Robins. (Robinson, 1906b).
- Ageratum pedatum* Ort., Hort. Reg. Bot. Matrit. 38. 1797, is *Florestina pedata* (Cav.) Cass. (Robinson, 1913b).
- Ageratum pohlianum* Baker in Martius, Fl. Bras. 6(2): 197. 1876, is not described well enough for proper disposition.
- Ageratum polyphyllum* Baker in Kew Bull. 139: 148. 1898, is *Ageratinastrum polyphyllum* (Baker) Mattf.
- Ageratum punctatum* Jacq., Hort. Schoenb. 3: 28. t. 300. 1798, is *Stevia serrata* Cav. (Robinson, 1913b).
- Ageratum purpureum* Aubl., Hist. Pl. Gui. Fr. 2: 800. 1775, is *Eupatorium* sp. (Robinson, 1913b).
- Ageratum purpureum* Ses. ex DC, Prodr. 5: 122. 1836, is *Stevia viscida* HBK or *Stevia pilosa* Lag. (personal communication, R. McVaugh).
- Ageratum quadriflorum* Blanco, Fl. Filip. 1: 624. 1837, is *Elephantopus spicatus* B. Juss. fide Villarii in Blanco, Fl. Filip., Ed. 3. Append. 114. 1880. (Robinson, 1913b).
- Ageratum riuale* Ses. & Moc., La Naturaleza, ser. 2. 1: 136. 1889, is *Pectis uniaristata* DC. (personal communication, R. McVaugh).
- Ageratum rubens* Viviani, Elenchus Pl. Hort. Bot. 9. 1802, is insufficiently described for proper disposition.
- Ageratum salicifolium* Coult. in J. D. Smith, Enum. Pl. Guatemal. 4: 72. 1895, is *Alomia guatemalensis* Robins. (Robinson, 1913b).
- Ageratum sandwichense* Levl., Repert. Spec. Nov. Regni Veg. 11: 63. 1913, is excluded because of its capillary pappus, but its proper disposition needs study. A type, *Fauri* 940, was seen (P) in 1966.
- Ageratum serratum* Glaziou, Bull. Soc. Bot. France 55(3): 382. 1909, is a *nomen nudum*.
- Ageratum sessilifolium* Schauer, Linnaea 19: 715. 1847, is *Trichocoronis sessilifolia* (Schauer) Robins. (Robinson, 1906b).
- Ageratum sordidum* Blake, Contr. U. S. Natl. Herb. 20(13): 534. 1924, is *Oxylobus glanduliferus* (Sch. Bip.) Gray (Robinson, 1913b).
- Ageratum striatum* Ses. & Moc., La Naturaleza, ser. 2. 1: 136. 1889, is probably *Stevia serrata* Cav. (personal communication, R. McVaugh).
- Ageratum strictum* Sims, Bot. Mag. t. 2410. 1823, is *Adenostemma lavenia* (L.) Kuntze (Robinson, 1913b).
- Ageratum viscosum* Ort., Hort. Reg. Bot. Matrit. 37. 1797, is *Stevia salicifolia* Cav. (Robinson, 1913b).
- Ageratum viscosum* Ses. & Moc., La Naturaleza, ser. 2. 1: 135. 1889, is *Stevia* sp. (personal communication, R. McVaugh).
- Ageratum wrightii* Torrey & Gray ex Gray, Proc. Amer. Acad. Arts 1: 46. 1848, is *Trichocoronis wrightii* (T. & G.) Gray.
- Phalacraea latifolia* DC. and *P. coelestina* Regel are given in lists of synonymy under *Ageratum conyzoides* L. by Hooker & Jackson (1893) and Vilmorin (1896) respectively. These names, I feel, should not be included in lists of synonyms under any *Ageratum* species because *Phalacraea* has the following characteristics, none of which occur in *Ageratum*: laterally compressed achenes, 3-ribbed involucre bracts, corolla tubes pilose-hispid at the base, lack of a pappus, and apical anther appendages (cf. Delessert, 1839; and Regel, 1854).

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